SOME CONTRIBUTIONS TO BIOMATHEMATICS

By

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INDIAN INSTITUTE OF TECHNOLOGY, KANPUR

JULY, 1979

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A Thesis Submitted
In Partial Fulfilment of the Requirements
for the Degree of
DOCTOR OF PHILOSOPHY

By

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to the
DEPARTMENT OF MATHEMATICS
INDIAN INSTITUTE OF TECHNOLOGY, KANPUR

JULY, 1979

MATH-1979-D-KHA-SOM

CERTIFICATE

This is to certify that the work presented in thesis entitled 'SOME CONTRIBUTIONS TO BIOMATHEMATICS' by Mr. Qamar Jalil Ahmad Khan has been carried out under my supervision and that this has not been submitted elsewhere for a degree or diploma.

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ACKNOWLEDGEMENTS

I am extremely grateful to Dr. J.N. Kapur, Ph.D., F.A.Sc., F.N.A.Sc., F.I.M.A., Professor and Head of Maths. Department, I.I.T. Kanpur, for his affectionate encouragement, help, supervision and guidence in the preparation of the thesis. Without his critical reviews, invaluable suggestions and constant encouragements, it would not have been possible for me to accomplish this work.

I also wish to express my sincere gratitude to Dr. J.B. Shukla for the encouragement which I have been receiving from him.

To all my colleagues and specially to Mohd. Saleem, Mohd. Amin Sofi, Meeraj Uddin and B. Kunwar, I am very thankful for their help and encouragement.

I wish to extend my sincere thanks to the authorities of I.I.T. Kanpur for providing me facilities and fellowship awarded to me during my research. I also wish to thank the CSIR for providing me a fellowship during the first two years of my research.

Finally, I thank Mr. G.L. Misra, Mr. S.K. Tewari for efficient typing of this thesis, Mr. B.N. Srivastava for drawing the graphs and to Mr. A.N. Upadhyay for a careful cyclostyling of the thesis.

I.I.T. Kanpur
July 1979.

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CONTENTS

PAGE

CHAPTER - 1

INTRODUCTION

The present thesis makes contributions to the following five areas of mathematical biosciences.

(a) Mathematical Models for Population Growth

(b) Difference Equations Models in Ecology and Epidemics

(c) Relative Stability of Difference and Differential Equation Systems

(d) Application of Bifurcation Theory to Population Models

(e) Transition to Stochastic Models from Deterministic Models.

These contributions are given in chapter II-VI of the present thesis.

In Chapter II, we give more than half a dozen models for growth of populations of microorganisms. A microbe or a microorganism is too small to be seen by the naked eye and is less than 0.1 mm of diameter. However inspite of their small size, these microbes play an important role in the following disciplines:

(1) <u>Fermentation technology</u> where microorganisms are used for producing foods, beverages, antibiotics, vitamins, plant growth regulators, flavour enhancing compounds, amino acids, enzymes, polysaccharides, single cell proteins and so on.

(2) Sanitary and Environmental Engineering where microorganisms are used to reduce water pollution.

(3) Ore and Fuel Processing where microorganisms can be used to leach certain undesirable substances from ores e.g. they can be used to remove sulphur from coal.

(4) Bioconversion of Solar Energy where microorganisms can be used to first absorb solar energy and then they can be used as a fuel.

Our models are based on the experimentally determined nature of the function $k(c)$ where $k(c)$ is the specific growth function for microorganism or i.e. it is growth rate per microorganism and c is the concentration of the substrate from which the microbe derives the nourishment.

In the literature various forms are given for $k(c)$.

(a) Monod's function [1949]
(b) Teisser's Function [1942]
(c) Jost et al Function [1973]
(d) Shehata and Marr Function [1971]
(e) Dabes et al Function [1973]
(f) Moser's Function [1958].

Corresponding to each of these, we get a mathematical model to determine the population size $N(t)$ as a function of time. We find that in each case, the population has a limiting size and each growth curve has a point of inflexion.

Since most of the growth curves observed in practice have these features, the large variety of models gives us a good scope for fitting of data for different microbes and different substrates. We have also investigated general theoretical models which give rise to sigmoid growth curves with points of inflexion and limiting population sizes.

All the models in the second chapter are in terms of differential equations. However difference equation models are also used in population dynamics, ecology, epidemics etc. These are relatively simpler to understand and manupulate because these do not require a knowledge of calculus. These models can be understood even by non-mathematically oriented demographers, ecologists and epidimologists and can enable all college students to understand the great problems in this discipline. Both these types of models have been used in the literature and both can represent reality. In fact the validity of a model can only be tested by comparing its predictions with actual observations. Moreover differential equations are usually obtained by first writing difference equations and then using a limiting process. For numerical integration we have again to transform the differential equations to difference equations. In recent years there has been an increased interest in modelling ecosystem in terms of difference equations [74]. This interest stems from the recognition that many species have important discrete components

in their life histories, such as synchronized breeding, seasons and seasonal death. Difference equation models are more or less analogous to the more common differential equation models.

In Chapter III we accordingly investigate the following difference equations models.

1. Growth of a population
2. Growth of a population with limited resources
3. Influence of pollution on population growth
4. Influence of age structure
5. An alternative method of taking age structure into account
6. Prey-Predator and Host-Parasite models
7. Interaction between predators and prey
8. Leslie's equations
9. Competition between two species
10. Competition among three species
11. Epidemic model without removal
12. Epidemic model with removal
13. Growth of population with time-delay
14. Growth of population with time-delay with limited resources
15. Prey-Predator model with time-delay.

In each of these we have drawn graphs and discussed important conclusions.

One of the important problems in ecology is the stability of the system. While both difference and differential

equations can be used to model ecosystems, these models may not produce identical stability behaviour for corresponding models. Corresponding to difference equation model, we can try to obtain a differential equation model, by using a limiting process and corresponding to each differential equation model we may try to obtain a difference equation model by converting differential equation to difference equation. In Chapter IV, we discuss the relative stability of some correspondence models. For defining the analogous discrete system, May [1973] has replaced the derivative by a forward difference operator with step size $h > 0$ so that

$$\frac{dN_j(t)}{dt} \approx \frac{1}{h}(T-1)\,N_j$$

where

$$TN_j(t) = N_j(t+h)$$

and time has been normalised so that $h = 1$ May [1973] has stated that:

> ''It is widely understood that difference equations tend to be less stable than their differential equation twins, because the finite time lapse between generations of growth will have the destabilizing effects associated with any time leg in an interacting system. Our discussion makes it explicit, clearly stability of the difference equations system implies stability of the differential equation one, but the converse is not necessarily true''.

lag

However Driessche [1974], using the operational rule

$$(T-1)N_j \approx \frac{h}{2}(T+1)\frac{dN_j}{dt}$$

has shown that the resulting analogous discrete system is as stable as the differential equation system.

In this chapter we examine the operational rule

$$(T-1)N_j \approx \frac{h}{\rho+1}(1+\rho T)\frac{dN_j}{dt}$$

where ($\rho \neq -1$) is a parameter, to compare the stability of the continuous and discrete models. The results of Driessche [1974] and May [1973] should follow as particular cases of ours and we may expect to get additional insight by using other values of ρ. We have shown that the relative stability of the difference and differential equation models depends on the operator used and we have demonstrated a class of operators for which difference equation model is more stable than the differential equation twin. This discussion illustrated with an age-structured population model with three age-groups. These three age groups are the pre-reproductive, the reproductive and the post-reproductive groups.

In Chapter V bifurcation theory is used to discuss the stability of some biological models. Bifurcation theory made significant progress and has found applications in various established fields and to many new engineering sciences. Bifurcation theory has been widely acclaimed and has found

fruitful application in theoretical biology. It is of particular interest in bifurcation theory to study how the solution and their multiplicity changes as a parameter varies. Nature of the equilibrium point changes when parameter values changes slightly in this case. For two dimensional case if the roots are $V \pm i\omega$, we get an unstable focus if $V > 0$, a centre if $V = 0$ and a stable node if $V < 0$. V is a function of the parameters and for some values of the parameter, V can be zero. A slight change in the value of the parameters would change the nature of the equilibrium. In this chapter, a set of conditions for a pair of eigenvalues of a stability problem matrix to be purely imaginary are obtained. These conditions are applied to discuss the existence of bifurcation point for (i) time-delay prey-predator model and (ii) growth of a single population under the effect of pollution.

Just as there is a correspondence between differential equation and difference equation models, there is also correspondence between deterministic and stochastic models. Corresponding to a given deterministic model in terms of differential equation, we can find a stochastic model. In general we can get a system of differential-difference equation for this stochastic model and can solve the problems by first solving a partial differential equation for the generating function. We find a number of such partial differential equations in the sixth chapter but unfortunately most of these

appear to be intractable either because these equations are non-linear or because the initial and boundary conditions are not sufficient or because the partial differential equation involve unknown probabilities. Here the partial differential equation have been used to determine some interesting relations between the expected values of the variables in some special cases for the some of the models discussed.

The work done in the present thesis has been published or accepted for publication or communicated for publication in the form of the following papers.

(1) Some Mathematical Models For Population Growth published in Indian J. Pure Appl. Math., Vol. 10, No. 3, p. 277-286, March 1979.

(2) Bifurcation Theory For Two Population Models published in Indian J. Pure Appl. Math., Vol. 9, No. 8 (1978), pp. 787-796.

(3) Relative Stability of Difference And Differential Equations System published in National Academy of Science Vol. 2, No. 4, April 1979.

(4) Difference Equation Models in Ecology and Epidemics (To be communicated).

(5) Some Mathematical Models of Population Growth - II (To be communicated).

(6) Stability of Differential Equation and Difference Equation System (Communicated for publication).

CHAPTER - 2

MATHEMATICAL MODELS FOR POPULATION GROWTH

2.1 INTRODUCTION

Among the many aspects of a population, ecologists are concerned with its growth taking into account its fertility, mortality, growth form and regulation (fluctuations, oscillations, dispersal etc.). They are also interested in inter and interaspecific interactions among populations (cooperation, predation, competition etc.). Since its inception, this field of population dynamics has had a strong mathematical orientation in formulating and testing descriptive and predictive models.

It was observed by Malthus [1798] many years ago that the human population tends to grow in geometrical progression or the rate of population increase is proportional to the population itself.

By 1830's it was noted by several persons that the strength of exponentiation process seems to be declining. Various hypotheses concerning the resistance or the obstacles put in the way of the indefinite development of the population can be made. Quetlet suggested that saturation might even be expected. Verhulst [1838] produced a correction factor to the Malthus equation which would imply saturation

$$\frac{dN}{dt} = KN \left[1-(N/\theta)\right], \tag{1}$$

where θ is the saturation population. Of course as $\theta \to \infty$ this reduces to Malthus equation.

The first one to attempt an adequate mathematical representation of the normal rate of growth of the population of united states was Pritchett. Taking the census data from 1790 to 1880, Pritchett fitted by the method of least squares the following equation

$$P = A + Bt + Ct^2 + Dt^3 \tag{2}$$

where P represents the population and t the time from some assumed epoch. Pritchett got a very accurate representation of the population between the dates covered. As will presently appear, this curve did not give, even within the period covered as accurate results as a really satisfactory curve should have done.

During the early 1920's Pearl and Reed [1924] analyzed the population growth of many European countries by employing the form

$$N(t) = C_0 + C_1 / \left[1 + C_2\, e^{-\alpha t}\right] \tag{3}$$

The extra parameter C_0 was introduced so that the two growth regims could be characterized by one equation. C_0 is the value of $N(t)$ as $t \to -\infty$.

A family of emperical curves which saturates either more slowly or more rapidly than the initial form of the rise can be derived from the following generalization of the Verhulst equation [1838]

$$\frac{dN}{dt} = KN\ [1 - (N/\theta)^{\alpha}]/\alpha \tag{4}$$

which is the same as (1) when $\alpha = 1$. As $\alpha \to 0$, (4) gives

$$\frac{dN}{dt} = -KN \log\ (N/\theta) \tag{5}$$

which is known in the population literature as the Gompertz [1825] equation. This equation never becomes popular because this was more difficult to fit by least squares to census data than was the Verhulst equation.

In view of fluctuating population driving forces, it would seem that a more appropriate model for population variation would be characterized by the equation

$$\frac{dN}{dt} = KN\ G(N/\theta) + N\ F(t) \tag{6}$$

where $F(t)$ is considered to be a random function of time which reflects changes in the economy and attitudes.

One of the most successful models for explaining the growth of populations of bacteria and even of humans is the so-called logistic model (1). Its characteristic features are:

(i) a limiting population size and ultimate zero growth rate

(ii) an S-shaped graph with a point of inflexion.

Many observed populations show these features but do not fit the logistic model very well. Smith [1963] gave another model with these features giving a better fit in some situations. In the present chapter half a dozen new models for microbial population growth are given. They are based on the experimentally determined laws for the dependence of the specific growth rate of a population on the concentration of rate-limiting substrate. It is shown that though these laws are quite different, they all lead to logistic-type growth curves with points of inflexion and limiting population sizes.

2.2 IMPORTANCE OF MODELS OF POPULATION GROWTH

Actuaries and demographers are interested in models of growth for human population for predicting expected duration of life at various ages and for estimating future population trends (Pollard [1973]). Bioeconomists are interested in models of growth for populations of sheep, fish, forests and other renewable resources for the sake of their optimal exploitation (Clark [1976]). Medical scientists and biologists are interested in models of growth of bacterial populations for the sake of controlling diseases, and epidemics and for genetical studies. Chemical engineers are interested in models of growth of populations of all microorganisms for the role they play or can play in four major areas viz.

(i) Fermentation technology where microorganisms are used for producing foods, beverages, antibiotics, vitamins, plant growth regulators, flavour enhancing compounds, amino acids, enzymes, polysaccharides, single-cell proteins and so on.

(ii) Sanitary and environmental engineering where microorganisms are used to reduce water pollution.

(iii) Ore and fuel processing where microorganisms can be used to leach certain undesirable substances from ores e.g. they can be used to remove sulphur from coal

(iv) Bioconversion of solar energy where microorganisms can be used to first absorb it and they can be used as fuels. (Frederickson and Tsuchiya [1977]).

One specific example is the release of methane gas from bio-gas plant which is due to the action of microorganisms. For increasing the amount of gas released, it is necessary to understand the mutual relationships between the growth of microorganisms, the change in the substrate and the amount of gas produced.

2.3 THE LOGISTIC CURVE

The simplest growth model is

$$\frac{dN}{dt} = aN, \tag{7}$$

where $N(t)$ is the population at time t and a is the excess of births over deaths per unit time per individual. This

is known as law of Malthus and gives on integration

$$N(t) = N_o e^{at} \qquad (8)$$

This model is valid when there are unlimited resources available to the population. However limitation of resources suggest the introduction of an inhibiting term on the right hand side of (7) to take into account the competition for resources among members of the population. The simplest modified law is the logistic law

$$\frac{dN}{dt} = aN - bN^2 \qquad (9)$$

Integration of (9) gives

$$N = \frac{N_e}{1+(\frac{N_e}{N_o}-1)\, e^{-at}}, \quad N_e = \frac{a}{b} \qquad (10)$$

The logistic curve is S-shaped and has a point of inflexion when

$$N = \frac{a}{2b} = \frac{1}{2} N_e \qquad (11)$$

curve is shown in Figure 2.1 .

This law explains very well the growth of a bacterial colony in a nutrient medium or ~~broth~~, provided the initial noculum N_o is taken from an exponentially growing colony Gauss [1934], Rubinow [1975] . It has also been successfully used to fit data for human populations. Equation (9) is sometimes replaced by

$$\frac{dN}{dt} = a(t)N - b(t)\,N^2 \qquad (12)$$

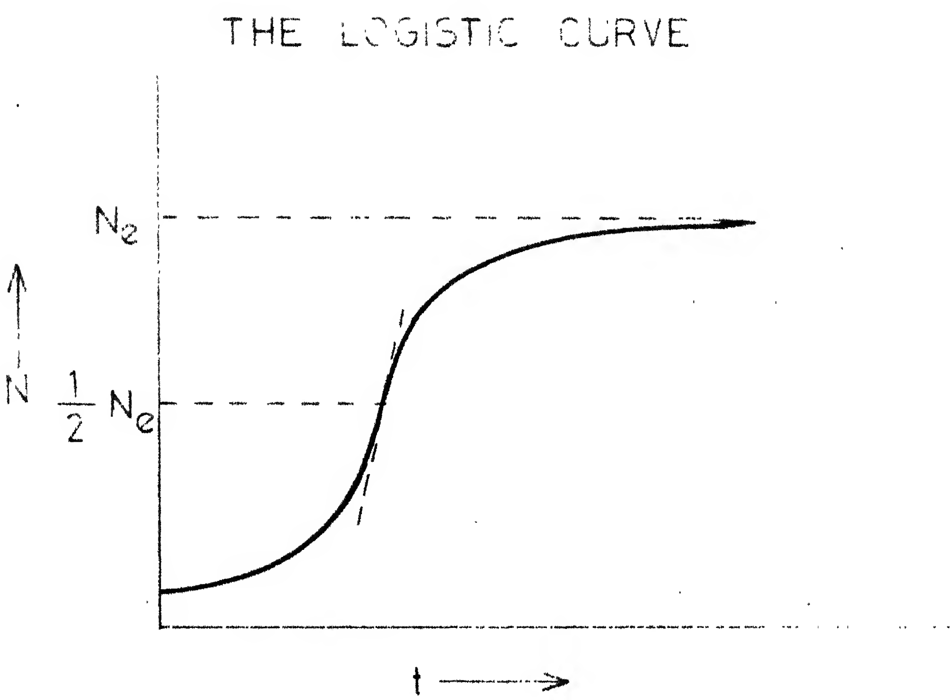


Fig. 2.1

which gives on integration

$$\frac{1}{N} = e^{-\alpha(t)} \left[\frac{1}{N_0} + \int_0^t e^{\alpha(t)} \, b(t) \, dt \right] \qquad (13)$$

where

$$\alpha(t) = \int_0^t a(t) dt \qquad (14)$$

2.4 MODEL OF SMITH

According to (9), $\frac{1}{N}\frac{dN}{dt}$ should be a linear function of N. Smith [1963] and Pielou [1969] found in his experiments on bacterial cultures that while the graph of N against t was a sigmoid or S-shaped curve, the graph of $\frac{1}{N}\frac{dN}{dt}$ against N was not a straight line but it was a concave curve. He argued that the term a-bN in (9) should be replaced by the rate of food supply not being used by the population i.e. it should be replaced by $\gamma(S-F)/S$ where F is the rate at which food is being used and S is the saturation rate. He assumed that

$$F = \lambda N + \mu \frac{dN}{dt} \qquad (15)$$

so that

$$\frac{1}{N}\frac{dN}{dt} = \gamma \frac{S-F}{S} = \frac{\gamma\left(\lambda K - \lambda N - \mu \frac{dN}{dt}\right)}{\lambda K} \qquad (16)$$

or

$$\frac{1}{N}\frac{dN}{dt} = \frac{\gamma(K-N)}{K+ \nu N}, \qquad (17)$$

where

$\nu = \frac{\gamma\mu}{\lambda}$. This model gave a good fit for his data. If $N_0 < K$, we find that $\frac{dN}{dt} > 0$, the population goes on increasing at a decreasing rate and ultimately as $N \to K$, the growth rate $\to 0$ so that K is the limiting size of the population. If $N_0 > K$, the population decreases to the limiting size K.

Also

$$\frac{1}{\gamma}\frac{d^2N}{dt^2} = \frac{-\nu}{(K+\nu N)^2}\left[(N+\frac{K}{\nu})^2 - K^2\left(\frac{1}{\nu}+\frac{1}{\nu^2}\right)\right]\frac{dN}{dt} \qquad (18)$$

so that there is a point of inflexion when

$$\frac{N}{K} = \left[\sqrt{\frac{1}{\nu}+\frac{1}{\nu^2}} - \frac{1}{\nu}\right] \qquad (19)$$

As $\nu \to 0$, $\frac{N}{K} \to \frac{1}{2}$ and as $\nu \to \infty$, $\frac{N}{K} \to 0$, so that the point of inflexion always occurs when N lies between 0 and K/2. As ν (or μ/λ) increases, the point of inflexion occurs for lower and lower values of N and if

$$\nu > \frac{1}{(\frac{N_0}{K})^2} - \frac{2}{(\frac{N_0}{K})}, \qquad (20)$$

there is no point of inflexion.

Thus Smith's model is likely to fit the data better when the point of inflexion on the sigmoid curve occurs before half the final population size is reached. We may also note that (17) has one parameter more than (9) and in fact includes (9) as a special case.

2.5 MODELS BASED ON MONOD's HYPOTHESIS

The law of growth is given by

$$\frac{dN}{dt} = K(C)N \tag{21}$$

where $K(C)$ is the specific growth rate and C is the concentration of the nutrient in the medium. Monod [1949, 50] and Rubinow [1975] assumed that the mathematical form for $K(C)$ was expressed by the Michaelis-Menten equation of enzyme kinetics i.e.

$$K(C) = Km \frac{C}{K+C} \tag{22}$$

The constant K_m is the maximum specific growth rate of the population, obtained when $C \gg K$, and the constant K is so-called Michaelis constant. K is the concentration of rate-limiting substrate at which $K(C)$ is one half of K_m. Many authors have found that Monod's law (22) does not fit growth rate data very well and they advanced other laws that fit data better.

2.6 MODEL BASED ON THE LAW OF TEISSER

Teisser [1942] found that equation

$$K(C) = K_m \left[1-\exp\left(- \frac{C \log 2}{K}\right)\right] \tag{23}$$

fitted his data quite well.

The law of growth in this case is given by

$$\frac{dN}{dt} = K_m \left[1 - \exp\left(- \frac{C \log 2}{K}\right)\right] N \tag{24}$$

The concentration C is reduced due to the consumption of the nutrient by the bacteria according to the law

$$\frac{dC}{dt} = -\frac{1}{y} K(C) N \tag{25}$$

so that consumption rate is being assumed proportional to both the population size of the bacteria and saturation function of the nutrient. Here y, the yield coefficient is the amount of biomass produced per unit amount of rate-limiting substrate consumed.

From equation (21) and (25)

$$\frac{dN}{dC} = -y \tag{26}$$

which gives on integration

$$N = y(C_1 - C) \tag{27}$$

where C_1 is the constant of integration.

From equation (24) and (27) we get

$$\frac{dN}{dt} = K_m \left[1 - \exp\left\{ -(C_1 - N/y) \frac{\log 2}{K} \right\} \right] N \tag{28}$$

After integrating equation (28), we find

$$\int_{X_0}^{X} \frac{dX}{X\left[1 - \exp\{-B(1-X)\}\right]} = \tau \tag{29}$$

where

$$C_1 y = \bar{C},\ \bar{K} = Ky,\ B = \frac{\bar{C}\log 2}{\bar{K}},\ \tau = K_m t,\ X = \frac{N}{\bar{C}} \tag{30}$$

and X_0 is the initial population.

Fig. 2.2 shows the population curves for different values of B when the initial population $X_0 = 0.1$.

A point of inflexion, which is the characteristic feature for the population growth can be found out by equating $\frac{d^2N}{dt^2}$ equal to zero.

Differentiating once the equation (21) we get

$$\frac{d^2N}{dt^2} = \left[-\frac{1}{y}K'(C)N + K(C)\right]\frac{dN}{dt} \tag{31}$$

For point of inflexion

$$yK(C) = NK'(C) \tag{32}$$

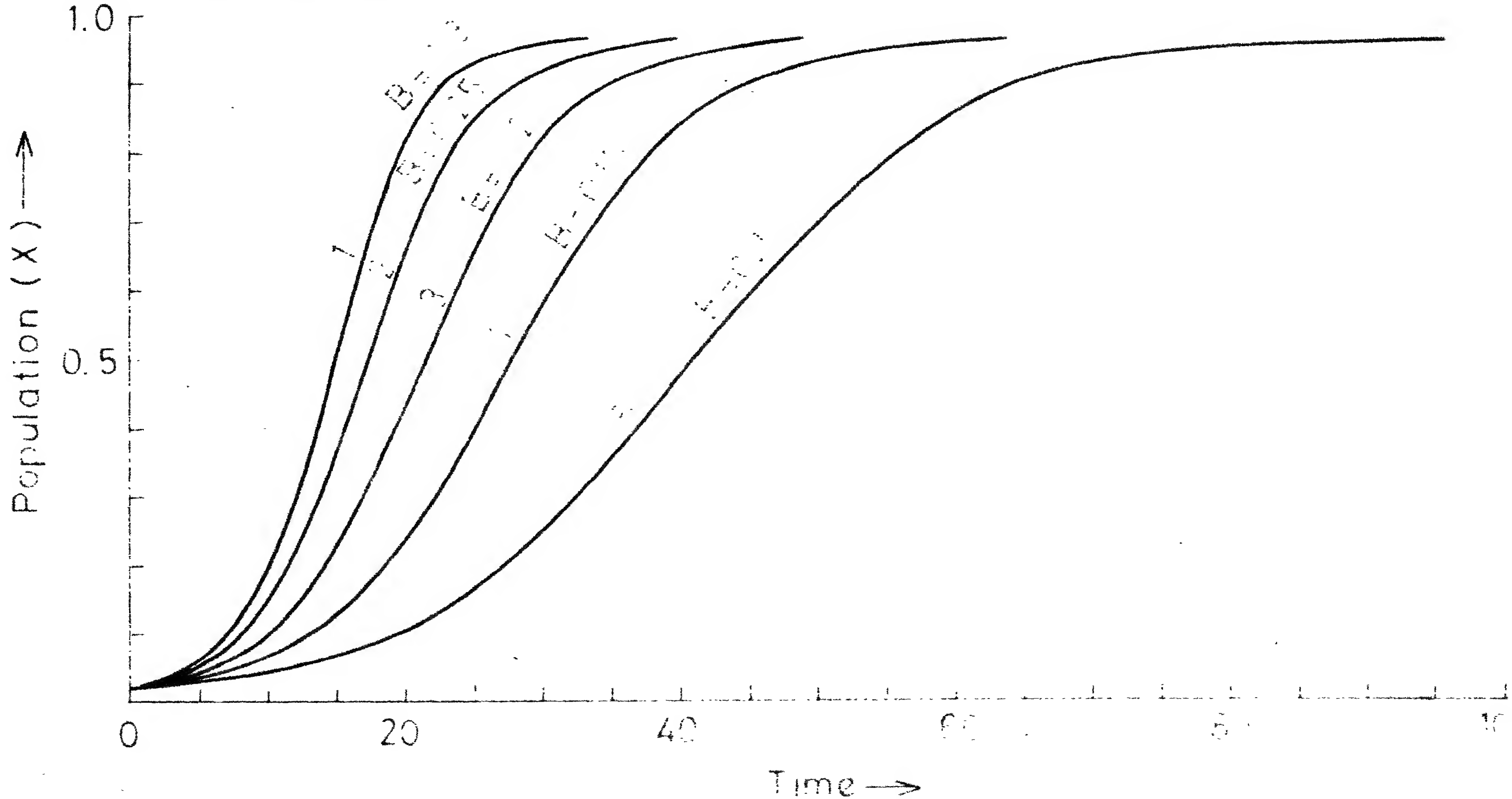
with the help of equation (23) and (32) we get the point of inflexion X^* will exist if

$$1-(BX^*+1)\,e^{-B(1-X^*)} = 0 \tag{33}$$

Applying condition (33), points of inflexion in the sub Figures of Figure 2.2 are given below

Sub Figures	B	Point of inflexion X^*
1	0.30	.518
2	0.25	.515
3	0.20	.512
4	0.15	~~.504~~ .509
5	0.10	.506

MODEL BASED ON THE LAW OF TEISSIER



When B is very small (33) gives, on neglecting B^2 and higher powers

$$1-2X^*-B\left[X^{*2}+\frac{1}{2}(1-X^*)^2\right]=0 \tag{34}$$

so that as $B \to 0$, $X^* \to \frac{1}{2}$

i.e. for very small values of B, point of inflexion will occur near half of the final population size.

Let

$$f(X) = 1-(1+BX)\, e^{-B(1-X)} \tag{35}$$

we give different values of X and find the sign of this function

$$f(0) = 1-e^{-B} > 0$$

$$f(1) = -B < 0$$

$$f(\tfrac{1}{2}) = 1-(1+\tfrac{1}{2}B)e^{-\frac{1}{2}B} = e^{-\frac{1}{2}B}\left[e^{\frac{1}{2}B}-(1+\tfrac{1}{2}B)\right] > 0 \tag{36}$$

These show that the point of inflexion X^* lies between 1 and $\frac{1}{2}$

so that

$$\tfrac{1}{2} < X^* < 1$$

As $\quad B \to \infty,\quad X \to 1$

<u>Thus a point of inflexion always exists and occur when the population size is more than half the final population size.</u>

2.7 MODEL BASED ON THE LAW OF JOST ET AL

Jost et al [1973] obtained from their experiments the law

$$K(C) = \frac{K_m C^2}{(K_1+C)\ (K_2+C)} \tag{37}$$

Growth of the population in this case is given by

$$\frac{dN}{dt} = \frac{K_m\ C^2}{(K_1+C)(K_2+C)}\ N \tag{38}$$

From equation (27) and (38), after integration we get,

$$\int_{X_o}^{X} \frac{(H-\bar{C}X)(G-\bar{C}X)}{\bar{C}^2 X(1-X)^2}\ dX = \tau \tag{39}$$

where

$$C_1 y = \bar{C}$$

$$H = K_1 y + \bar{C},\ G = K_2 y + \bar{C},\ X = \frac{N}{\bar{C}}, \tau = K_m t \tag{40}$$

and X_o is the initial population

Figure 2.3 shows the population growth for different values of H and the initial population $X_o = .02$, $G = 3.0$, $\bar{C} = 1.0$.

Values of H in sub figures (1), (2), (3), (4) and (5) are 2.4, 2.6, 2.8, 3.0 and 3.2 respectively.

From equation (32) and (37) we find that point of inflexion will exist if

$$\phi(X) = (H-\bar{C}X)(G-\bar{C}X)(1-3X)+\bar{C}X\ (G+H-2\bar{C}X)(1-X)=0 \tag{41}$$

To find the point of inflexion, we give different values of X and see where the sign of the function change

For $X = \frac{1}{3}$

$$\phi(\tfrac{1}{3}) > 0$$

and for $X = 1$

$$\phi(1) < 0$$

<u>As such a point of inflexion always exist and occurs after one-third the final population size is reached</u>

If $G = H$, (41) gives

$$\phi(X) \equiv (G-\bar{C}X)\left[(G-\bar{C}X)(1-3X)+2\bar{C}X(1-X)\right]= 0 \tag{42}$$

Since $G > \bar{C}$, the first factor cannot be zero when $0 < X < 1$ and therefore the point of inflexion is given by

$$(\bar{G}-X)(1-3X) + 2X(1-X) = 0$$

or

$$X^2 + X(1-3\bar{G}) + \bar{G} = 0 \tag{43}$$

where $\bar{G} = \frac{G}{\bar{C}}$

Equation (43) has two positive roots, one greater than and the other less than unity. The latter root gives the point of inflexion. So that

$$X^* = \frac{1}{2}\left[(3\bar{G}-1) - \sqrt{(9\bar{G}-1)(\bar{G}-1)}\right] \tag{44}$$

For some different values of $\bar{G}$, the points of inflexion are

$\bar{G} = \frac{G}{\bar{C}}$	1	$\frac{3}{2}$	2
X^*	1	$\frac{1}{2}$	.44

and as $\bar{G} \to \infty$, $X^* \to \frac{1}{3}$.

Equation (44) determines the point of inflexion for the law

$$K(C) = \frac{K_m C^2}{(K_1+C)^2} \tag{45}$$

For the general law (37), the basic equation (41) is a cubic in X and its root lying between $\frac{1}{3}$ and 1 can be determined numerically. Using equation (41), the points of inflexion in sub figures of Figure 2.3 are given below

Sub Figures	H	Point of inflexion X^*
1	2.4	.4045
2	2.6	.4005
3	2.8	.397214
4	3.0	.3944
5	3.2	.3920

2.8 MODEL BASED ON THE LAW OF SHEHATA AND MARR

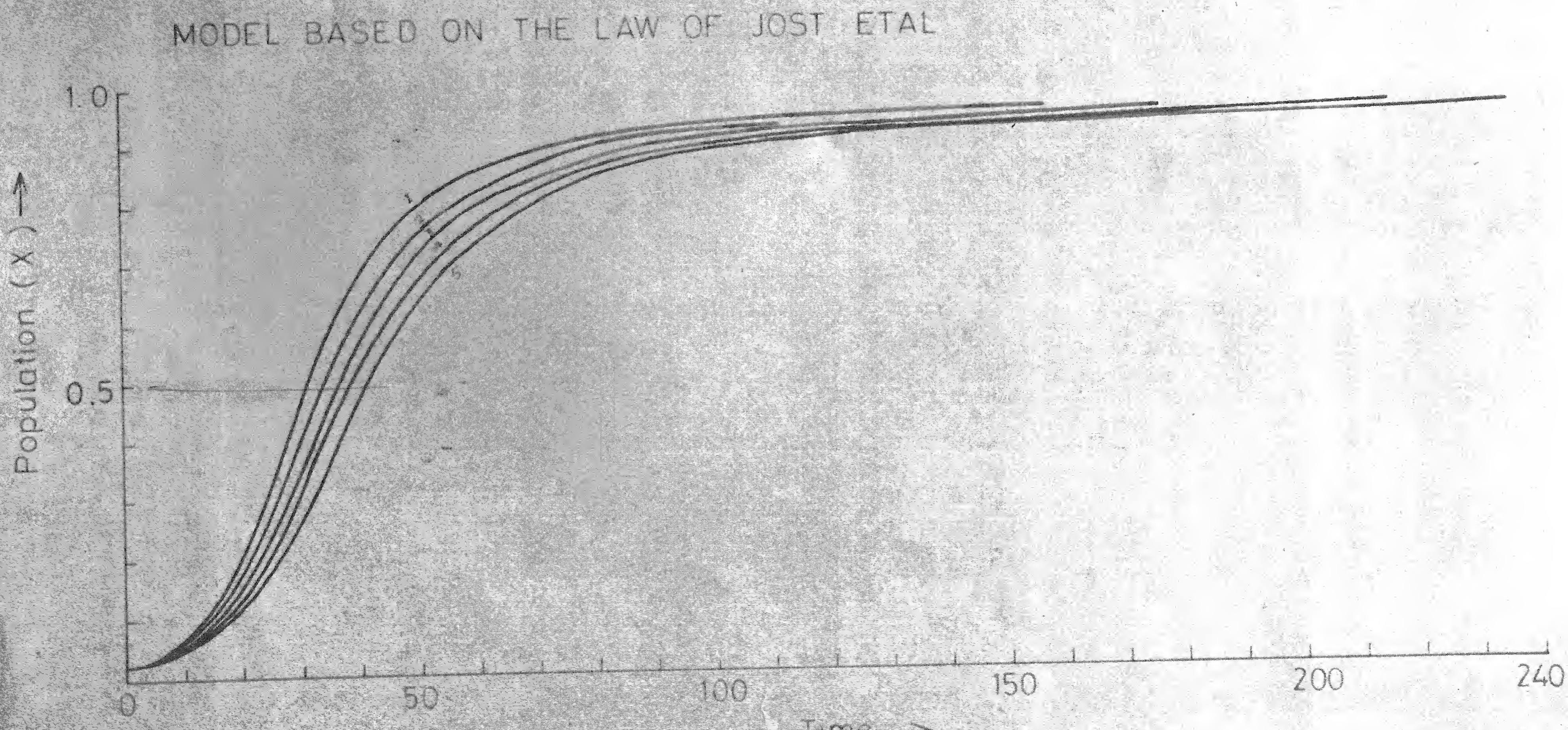
Shehata and Marr [1971] found from their experiments the law

$$K(C) = \frac{K_1 C}{K_1+C} + \frac{K_2 C}{K_2+C} \tag{46}$$

or a generalization of this involving the addition of further terms of the same form. They pointed out that this equation would arise if growth involved different but parallel process of substrate uptake.

The growth of the population in this case is given by

$$\frac{dN}{dt} = \left(\frac{K_1 C}{K_1+C} + \frac{K_2 C}{K_2+C}\right)N \tag{47}$$



MODEL BASED ON THE LAW OF JOST ETAL
1.0
0.5
Population (X) →
0
50
100
150
200
240
Time →

Fig. 2.3

From equation (27) and (47) after integration we get

$$\int_{X_0}^{X} \frac{(D-\bar{C}X)(E-\bar{C}X)}{X(1-X)\left[B-AX\right]} \, dX = \tau \tag{48}$$

where $D = K_1 y + \bar{C}$, $E = K_2 y + \bar{C}$, $X = \frac{N}{\bar{C}}$, $\tau = K_m t$

and A and B are positive constants

Figure 2.4 shows curves for

$X_o = .02$, $\bar{C} = 1.0$, $D = 2.2$, $E = 2.4$, $A = 5.0$ and

$B = 18, 16, 14, 12, 10$

The points of inflexion are given by

$$\psi(X) = K_1(\bar{E}-X)^2(2X\bar{D}-\bar{D}-X^2) + K_2(\bar{D}-X)^2(2\bar{E}X-\bar{E}-X^2) = 0 \tag{49}$$

where $\bar{D} = \frac{D}{\bar{C}}$, $\bar{E} = \frac{E}{\bar{C}}$

To find the point of inflexion, we give different values to X and see when sign of the function change

for $X = 0, \frac{1}{2}$, and 1

$$\begin{aligned} \psi(0) &= -K_1\bar{E}^2\,\bar{D} - K_2\bar{D}^2\,\bar{E} < 0 \\ \psi(\tfrac{1}{2}) &= -\frac{K_1}{4}(\bar{E}-\tfrac{1}{2})^2 - \frac{K_2}{4}(\bar{D}-\tfrac{1}{2})^2 < 0 \\ \psi(1) &= K_1(\bar{E}-1)^2(\bar{D}-1) + K_2(\bar{D}-1)^2(\bar{E}-1) > 0 \end{aligned} \tag{50}$$

since $\bar{D} > 1$, $\bar{E} > 1$

<u>As such a point of inflexion always exists and occur when the population has reached more then half the population size.</u> In fact $\psi(X)$ is negative when $X \leq \frac{1}{2}$, $\psi(1) > 0$, $\psi(\infty) < 0$ and as such $\psi(X) = 0$ has one positive root between $\frac{1}{2}$ and 1 and at least one positive root between 1 and ∞.

If $\bar{D} = \bar{E}$, then the root of (49) are

$$X = \bar{D},\ \bar{D} > 1,\ X = \bar{D} \pm \sqrt{\bar{D}^2 - \bar{D}} \qquad (51)$$

The point of inflexion occurs at

$$X^* = \bar{D} - \sqrt{\bar{D}^2 - \bar{D}} \qquad (52)$$

but in this case the law of Shehata and Marr reduces to Monod's law

For the Figure 2.4 the points of inflexion are given by

Sub Figures	B	Points of inflexion X^*
1	10.0	.552
2	12.0	.535
3	14.0	.513
4	16.0	.507
5	18.0	.505

2.9 MODEL BASED ON THE LAW OF DABES ET AL

Powell [1967] pointed out that a diffiusional resistance to substrate transfer through the medium around would affect the growth rate. When Mond's model was modified to account for this, Powell obtained

$$K(C) = \frac{K_m(K+L+C)}{2L}\left[1 - \sqrt{1 - \frac{4LC}{(K+L+C)^2}}\ \right] \qquad (53)$$

where L is the parameter having the dimension of concentration which depends on the diffusional resistance around the cell. Powell's equation reduces to that of Monod of L is set equal to zero.

MODEL BASED ON THE LAW OF SHEHATA AND MARR

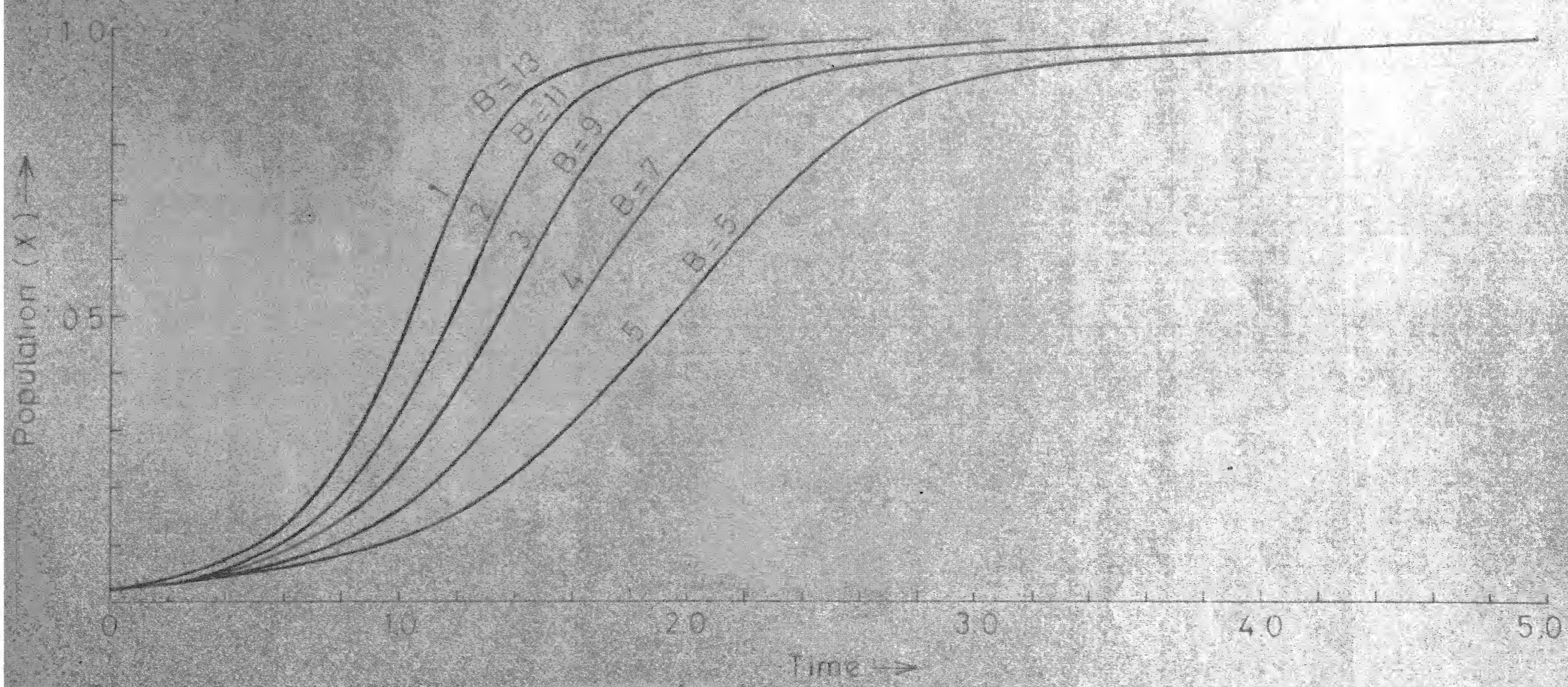


Fig. 2.4

Recently, Dabes et al [1973] have proposed a number of new growth rate equations

$$K(C) = \frac{B+AK_m+C-\sqrt{(B+AK_m+C)^2-4AK_m C}}{2A} \tag{54}$$

Growth of the population in Powell and Dabes models are similar. Here Dabe model is taken. From equation (21), (27) and (54), after integration we get

$$\int_{X_o}^{X} \frac{dX}{X[(H'-\bar{C}X)-\sqrt{(H'-\bar{C}X)^2-G'(1-X)}]} = \tau \tag{55}$$

where $\bar{C} = C_1 y$, $X = \frac{N}{\bar{C}}$, $\tau = K_m t$, (56)

$(B+AK_m)y + \bar{C} = H'$, $4AK_m\bar{C} = G'$ and X_o is the initial population.

Figure 2.5 shows the population growth for different values of H' when the initial population $X_o = .02$, $G' = 1.2$, $\bar{C} = 1.0$.

Values of H' for sub figures (1), (2), (3), (4) and (5) of Figure 2.5 are 2.4, 2.6, 2.8, 3.0 and 3.2 respectively.

From equation (32) and (54) we find that point of inflexion will exist if

$$2(H'-CX-1)\sqrt{(H'-CX)^2-G'(1-X)} + X[2C(H'-CX) - G'] - 2[(H'-CX)^2 - G'(1-X)] = 0 \tag{57}$$

using equation (57) we can find the point of inflexion of sub figures contained in Figure 2.5. These are given below

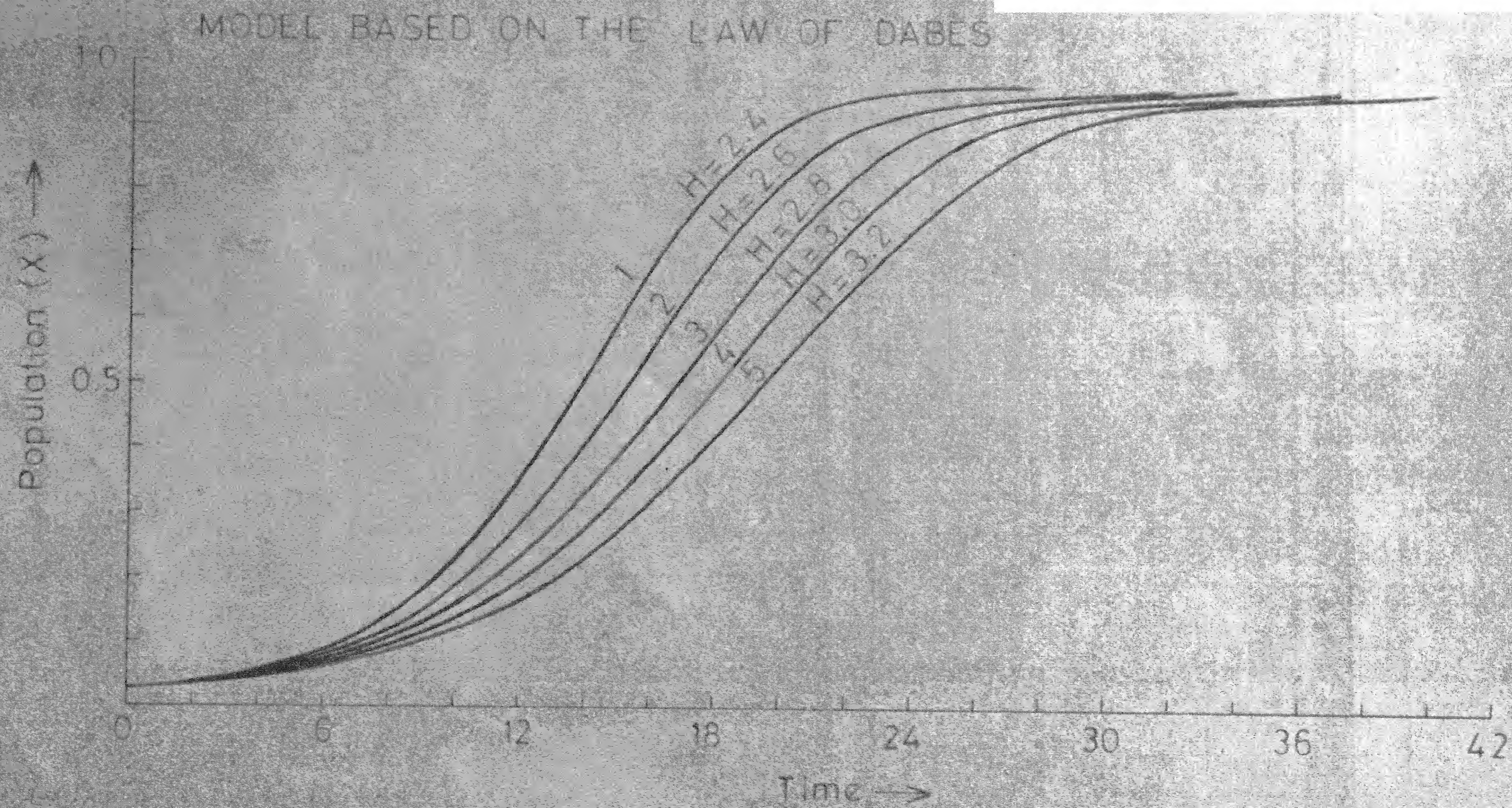

MODEL BASED ON THE LAW OF DABES
Population (X) →
1.0
0.5
0
6
12
18
24
30
36
42
Time →
1 H=2.4
2 H=2.6
3 H=2.8
4 H=3.0
5 H=3.2

Fig 2.6

Sub figures	H'	Point of inflexion
1	2.4	.5604
2	2.6	.5548
3	2.8	.5502
4	3.0	.5463
5	3.2	.5430

2.10 MODEL BASED ON THE LAW OF MOSER

We give here two more models of the same type based on consideration of enzyme kinetics and compare these with the existing models.

A more general form of (22) is given by Hill's equation or Moser law [1958]

$$K(C) = K_m \frac{C^n}{K^n + C^n} \tag{58}$$

From (21), (27), (58), we get

$$\frac{dN}{dt} = \frac{K_m (C_1 - N/y)^n N}{K^n + (C_1 - N/y)^n} = \frac{K_m (\bar{C} - N)^n N}{\bar{K}^n + (\bar{C} - N)^n} \tag{59}$$

where $\bar{K} = Ky^n$, $\bar{C} = C_1 y$ (60)

we note that

i) If $N_0 < \bar{C}$, then $\frac{dN}{dt} > 0$, N goes on increasing and as $N \to \bar{C}$, $\frac{dN}{dt} \to 0$ so that $\bar{C}$ is the limiting size of the population. In our model $\frac{dN}{dt}$ cannot be negative

ii) The graph of $\frac{1}{N}\frac{dN}{dt}$ against N is not a straight line but may be a concave or convex curve.

iii) There are two equilibrium points viz. $N = 0$ and $N = \bar{C}$ The first is unstable and the second is stable. If N is initially zero, it always remain zero, but if N_0 is slightly greater than zero, then N grows with time and approaches $\bar{C}$ asymptotically.

iv) $$\frac{d^2N}{dt^2} = K_m(\bar{C}-N)^{n-1} \frac{[(\bar{C}-N)^{n+1}+\bar{K}^n(\bar{C}-N)-nN\bar{K}^n]}{[\bar{K}^n+(\bar{C}-N)^n]^2}\frac{dN}{dt} \tag{61}$$

Let

$$f(N) = (\bar{C}-N)^{n+1} + \bar{K}^n(\bar{C}-N) - nN\bar{K}^n \tag{62}$$

$$= (\bar{C})^{n+1}\{(1-X)^{n+1}+A\,(1-\overline{n+1}\,X)\} = (\bar{C})^{n+1}\,\phi(X) \tag{63}$$

where

$$X = \frac{N}{\bar{C}}\,,\quad A = \frac{\bar{K}^n}{\bar{C}^n} = \frac{K^n}{C_1^n} \tag{64}$$

In general $X_o = \frac{N_o}{\bar{C}} << 1$ and we can assume

$$\phi(X_o) = (1-X_o)^{n+1}+A\,(1-\overline{n+1}\,X_o) > nAX_o \tag{65}$$

Also $\phi(1)$ is negative and so the population curve has a point of inflexion at X^* between X_o and 1. The position of the point of inflexion will depend on A and n.

For a given n, we can choose A so that the point of inflexion is at a given point X^* where $\frac{1}{n+1} < X^* < 1$

v) For a given observed population curve with a point of

inflexion and a limiting population size, $\bar{C}$ is given by the limiting population size, then $X_o = N_o/\bar{C}$ is given by the initial population size. The existence of the point of inflexion shows that $n > \frac{1}{X^*} - 1$ and then A is given by

$$A = \frac{(1-X^*)^{n+1}}{(n+1)X^*-1} \tag{66}$$

we can choose n to get best fit to the data.

vi) The model is more general than the logistic model as well as Smith's model in the sense that if can give population curves with points of inflexion both before and after $\bar{C}/2$ while logistic model gives a point of inflexion only at $\bar{C}/2$ and Smiths model gives only before $\bar{C}/2$. This is not surprising since our model is a four parameter model, whereas the earlier model were two and three parameter models respectively.

vii) From (59) and (64)

$$\frac{1}{X}\frac{dX}{d\tau} = \frac{(1-X)^n}{A+(1-X)^n} \tag{67}$$

where $\tau = K_m t$ (68)

Integrating

$$\int_{X_o}^{X} \left[\frac{A}{X(1-X)^n} + \frac{1}{X}\right] dX = \tau \tag{69}$$

when $n = 1$, this gives

$$(A+1) \log \frac{X}{X_o} + A \log \frac{1-X_o}{1-X} = \tau \tag{70}$$

If n is a positive integer greater than unity, we get

$$(A+1)\log\frac{X}{X_o} + A\log\frac{1-X_o}{1-X} + A\Big[\frac{1}{1-X} + \frac{1}{2(1-X)^2} + \dots$$

$$+ \frac{1}{(n-1)(1-X)^{n-1}}\Big]_{X_o}^{X} = \tau \qquad (71)$$

When n is not an integer, we have to integrate numerically. We note that τ increases with A, X and n and decreases with X_o.

Figures 2.6–2.9 show population growth curves for different values of A and n for $X_o = 0.1$.

From equation (63) we can see that point of inflexion will exist if

$$\phi(X) = (1-X)^{n+1} + A\,(1-\overline{n+1}\,X) = 0 \qquad (72)$$

Points of inflexion of Figures 2.6–2.9 are given below

$A=0.5, X_o=0.1$ FIG. [2.6]		$A=2.0, X_o=0.1$ FIG [2.7]		$A=3.0, X_o=0.1$ FIG [2.8]		$A=4.0, X_o=0.1$ FIG [2.9]	
n	Point of Inflexion	n	Point of Inflexion	n	Point of Inflexion	n	Point of Inflexio
.33	.860936	.33	.796977	.33	.78443	.33	.77737
.50	.792602	.50	.716881	.50	.70269	.50	.69477
.66	.735166	.66	.654111	.66	.63935	.66	.631168
1.0	.633975	1.0	.55051	1.0	.53589	1.0	.527864
2.0	.446426	2.0	.374183	2.0	.36216	2.0	.355629
3.0	.343102	3.0	.283030	3.0	.27324	3.0	.26794
4.0	.278310	4.0	.227509	4.0	.21933	4.0	.21491
5.0	.234002	5.0	.190172	5.0	.18316	5.0	.17939

MODEL BASED ON THE LAW OF MOSER

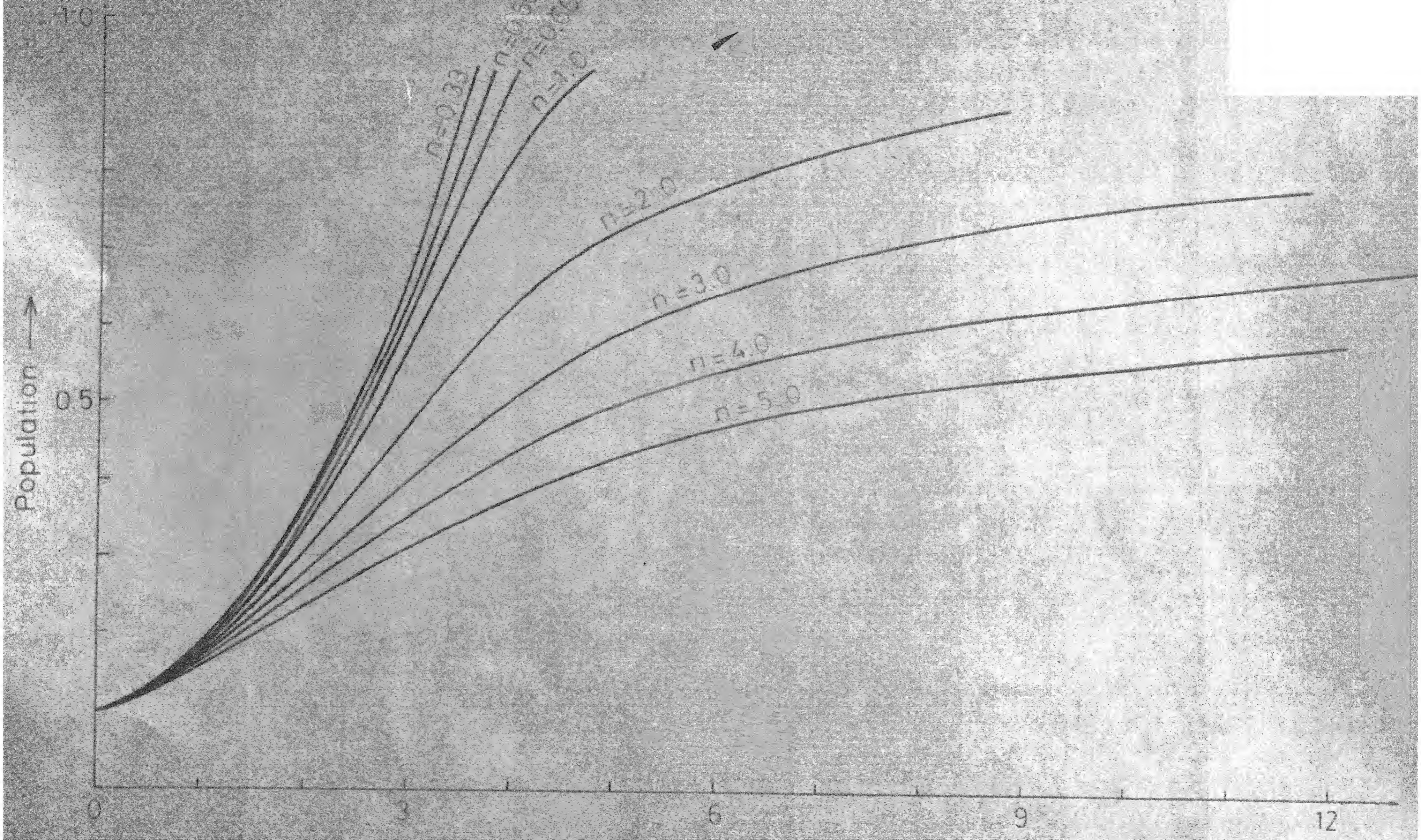


Fig. 2.6

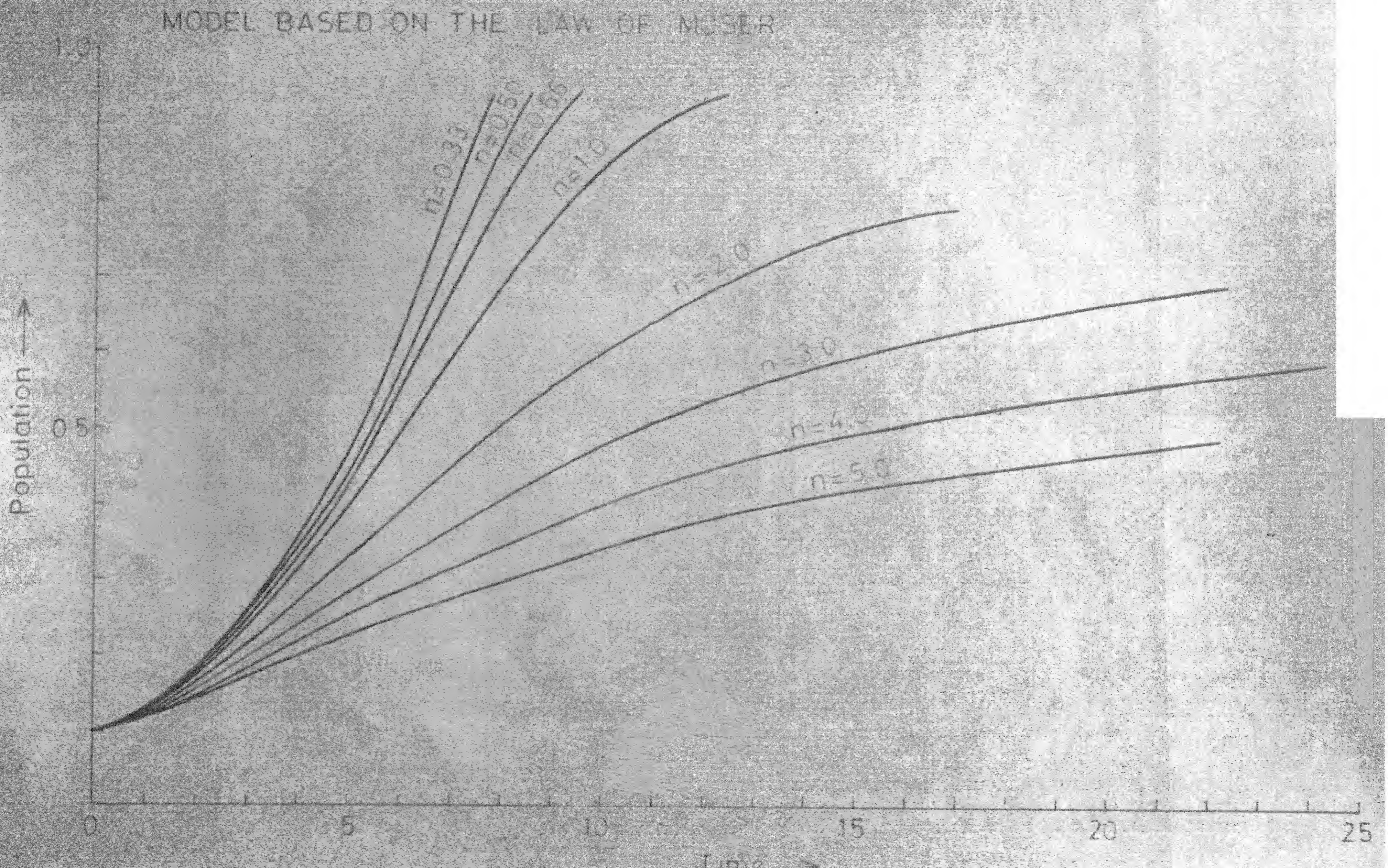

MODEL BASED ON THE LAW OF MOSER
1.0
0.5
Population →
n=0.33
n=0.50
n=0.66
n=1.0
n=2.0
n=3.0
n=4.0
n=5.0
0
5
10
15
20
25
Time →

Fig 2.7

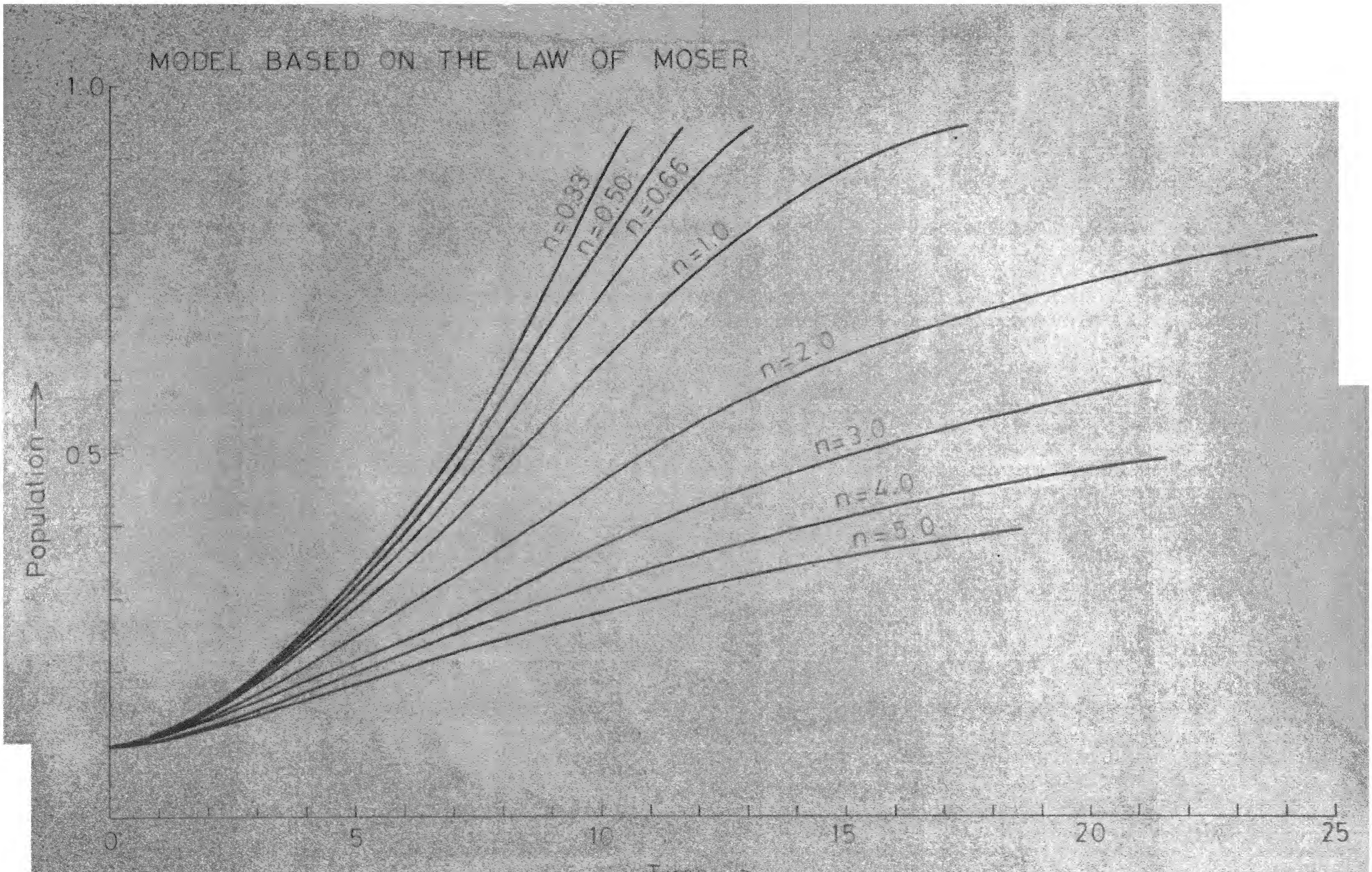

MODEL BASED ON THE LAW OF MOSER
1.0
0.5
Population ⟶
n=0.33
n=0.50
n=0.66
n=1.0
n=2.0
n=3.0
n=4.0
n=5.0
0
5
10
15
20
25
Time ⟶

Fig 2.8

MODEL BASED ON THE LAW OF MOSER

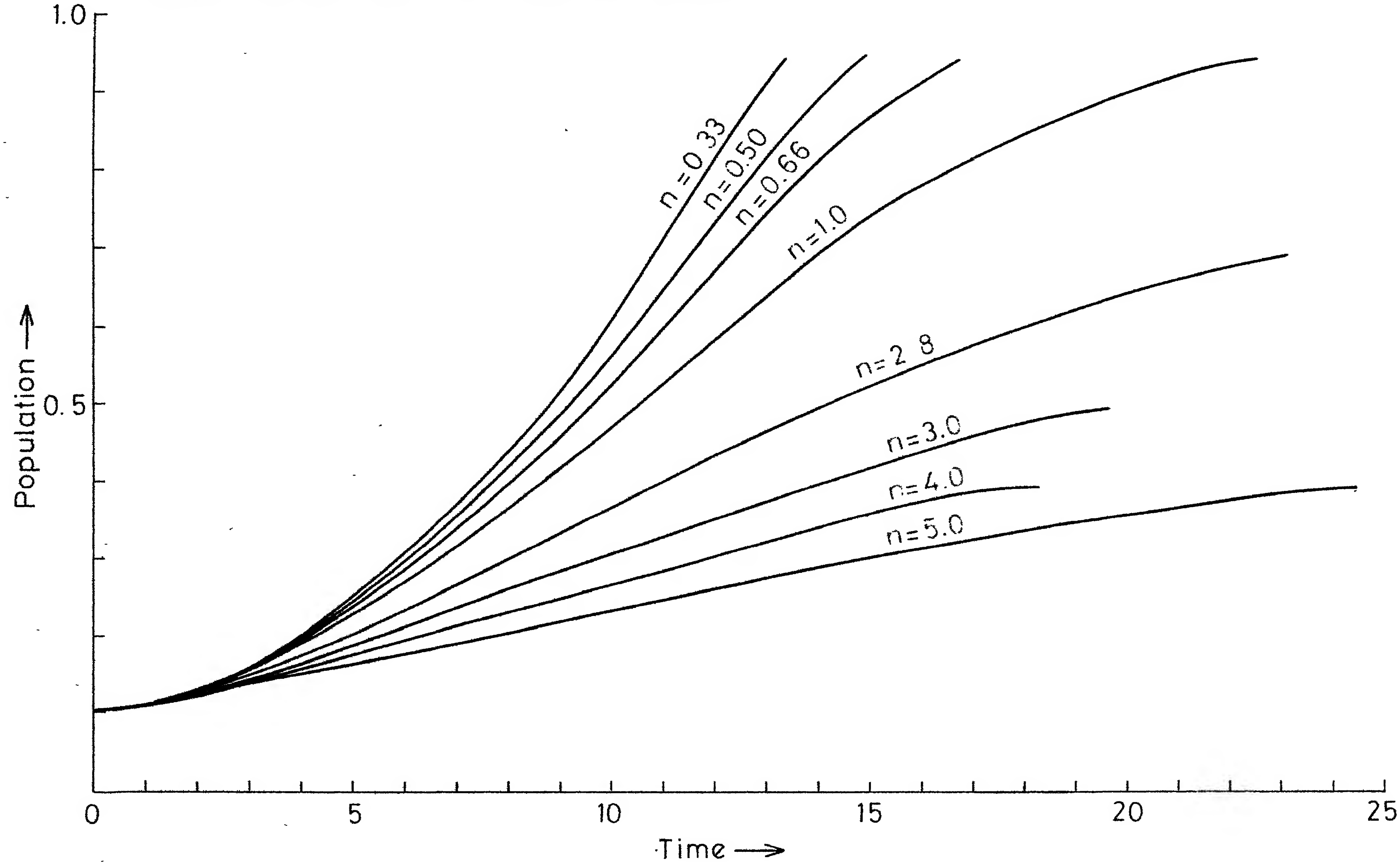


Fig. 2.9

2.11 ANOTHER POPULATION MODEL

Another equation for enzyme moderate reaction is

$$K(C) = K_m \frac{C(1+C)^3 + BC^4}{(1+C)^4 + BC^4} \tag{73}$$

From (21), (27), (60), (64) and (73)

$$\frac{dX}{d\tau} = \frac{(1-X)X[(z+1-X)^3+B(1-X)^3]}{(z+1-X)^4 + B(1-X)^4} \tag{74}$$

where

$$z = \frac{Y}{C} \tag{75}$$

Equation (74) can be easily integrated by quadrature.

For the point of inflexion we find

$$\frac{d^2X}{d\tau^2} = \frac{\psi(X)\,\frac{dX}{d\tau}}{[(z+1-X)^4+B(1-X)^4]^2} \tag{76}$$

where

$$\begin{aligned}\psi(X) = {} & [(z+1-X)^4+B(1-X)^4] \times [\{(z+1-X)^3(1-X) + B(1-X)^4\} \\ & - X\{(z+1-X)^3+3(1-X)(z+1-X)^2+ 4B(1-X)^3\}] \\ & + X\,[\{(1-X)(z+1-X)^3+ B(1-X)^4\} \times \{4(z+1-X)^3+4B(1-X)^3\}]\end{aligned} \tag{77}$$

so that

$$\psi(1) = - z^7 < 0 \tag{78}$$

Also $\psi(X_0) > 0$ if X_0 is sufficiently small. As such the population curve is an S-shaped curve with a limiting population size and each curve has in general a point of inflexion.

We have got here a three-parameter family of curves

Figures 2.10-2.13 show populations curves for different values of B and Z. Points of inflexion in these figures will exist if $\psi(X) = 0$ where $\psi(X)$ is taken from equation (77).

Points of inflexion for the Figures 2.10-2.13 different values of B and Z are given below.

FIG. 2.10 $B=.33, X_0=0.1$		FIG. 2.11 $B=0.5, X_0=0.1$		FIG. 2.12 $B=1.0, X_0=0.1$		FIG. 2. $B=2.0, X_0=$	
z	Point of Inflexion	z	Point of Inflexion	z	Point of Inflexion	z	Point Infle
.05	.265	.05	.2794	.05	.31203	.05	.355
0.1	.291	0.1	.3029	0.1	.3308	0.1	.369
0.2	.3494	0.2	.3568	0.2	.3755	0.2	.404

2.12 <u>GENERAL CLASS OF MODELS WITH POINTS OF INFLEXION</u>

Besides the logistic and Smith's models, we have given si more models of population growth based on experimental laws connecting specific growth rate with the concentration of the rate-limiting substrate. Though these laws are different, yet they lead to similar population growth curves. This is not entirely unexpected behaviour. These laws are based on laboratory experiments with microorganism thriving on one rate-limiting substrate. With different microorganism and different substrate, the laws can be somewhat different.

We now investigate mathematically general class of model with the same feature viz point of inflexion and limiting

We have got here a three-parameter family of curves

Figures 2.10–2.13 show populations curves for different values of B and Z. Points of inflexion in these figures will exist if $\psi(X) = 0$ where $\psi(X)$ is taken from equation (77).

Points of inflexion for the Figures 2.10–2.13 different values of B and Z are given below.

FIG. 2.10		FIG. 2.11		FIG. 2.12		FIG. 2.13	
$B=.33, X_0=0.1$		$B=0.5, X_0=0.1$		$B=1.0, X_0=0.1$		$B=2.0, X_0=0.1$	
z	Point of Inflexion	z	Point of Inflexion	z	Point of Inflexion	z	Point of Inflexio
.05	.265	.05	.2794	.05	.31203	.05	.3559
0.1	.291	0.1	.3029	0.1	.3308	0.1	.3699
0.2	.3494	0.2	.3568	0.2	.3755	0.2	.40438

2.12 GENERAL CLASS OF MODELS WITH POINTS OF INFLEXION

Besides the logistic and Smith's models, we have given six more models of population growth based on experimental laws connecting specific growth rate with the concentration of the rate-limiting substrate. Though these laws are different, yet they lead to similar population growth curves. This is not entirely unexpected behaviour. These laws are based on laboratory experiments with microorganism thriving on one rate-limiting substrate. With different microorganism and different substrate, the laws can be somewhat different.

We now investigate mathematically general class of model with the same feature viz point of inflexion and limiting

ANOTHER POPULATION MODEL

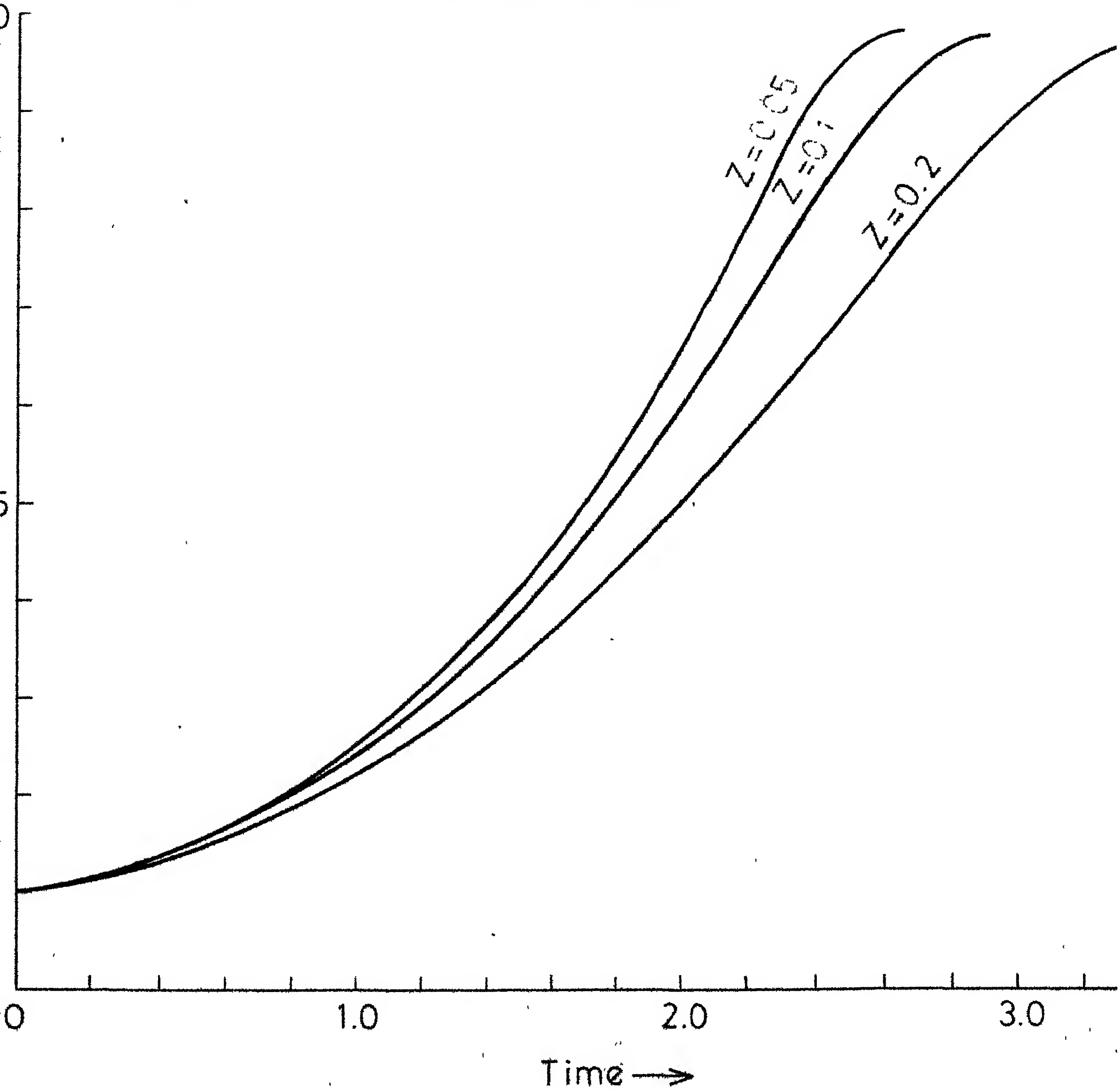


Fig. 2.10

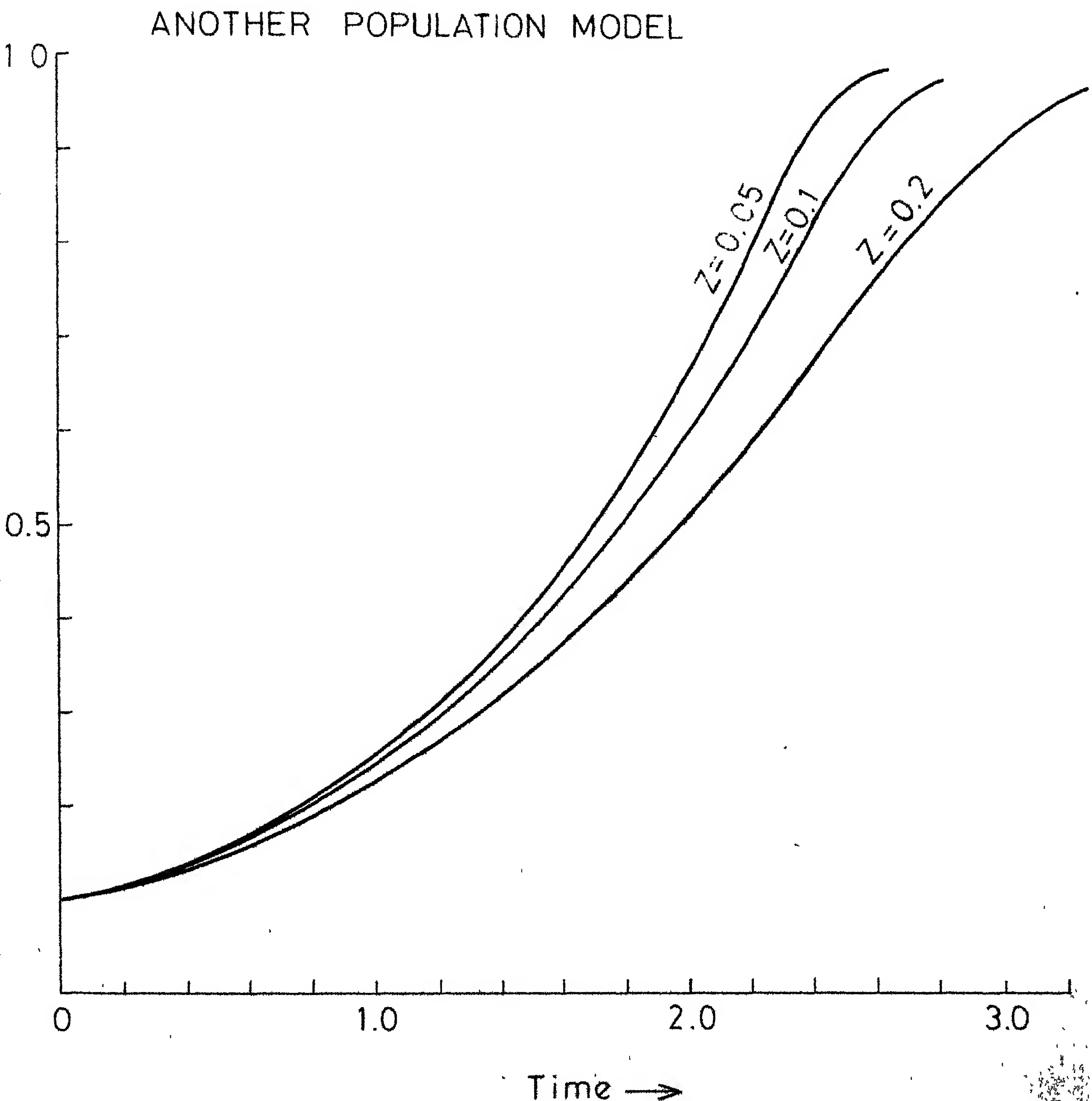


Fig 2.11

ANOTHER POPULATION MODEL

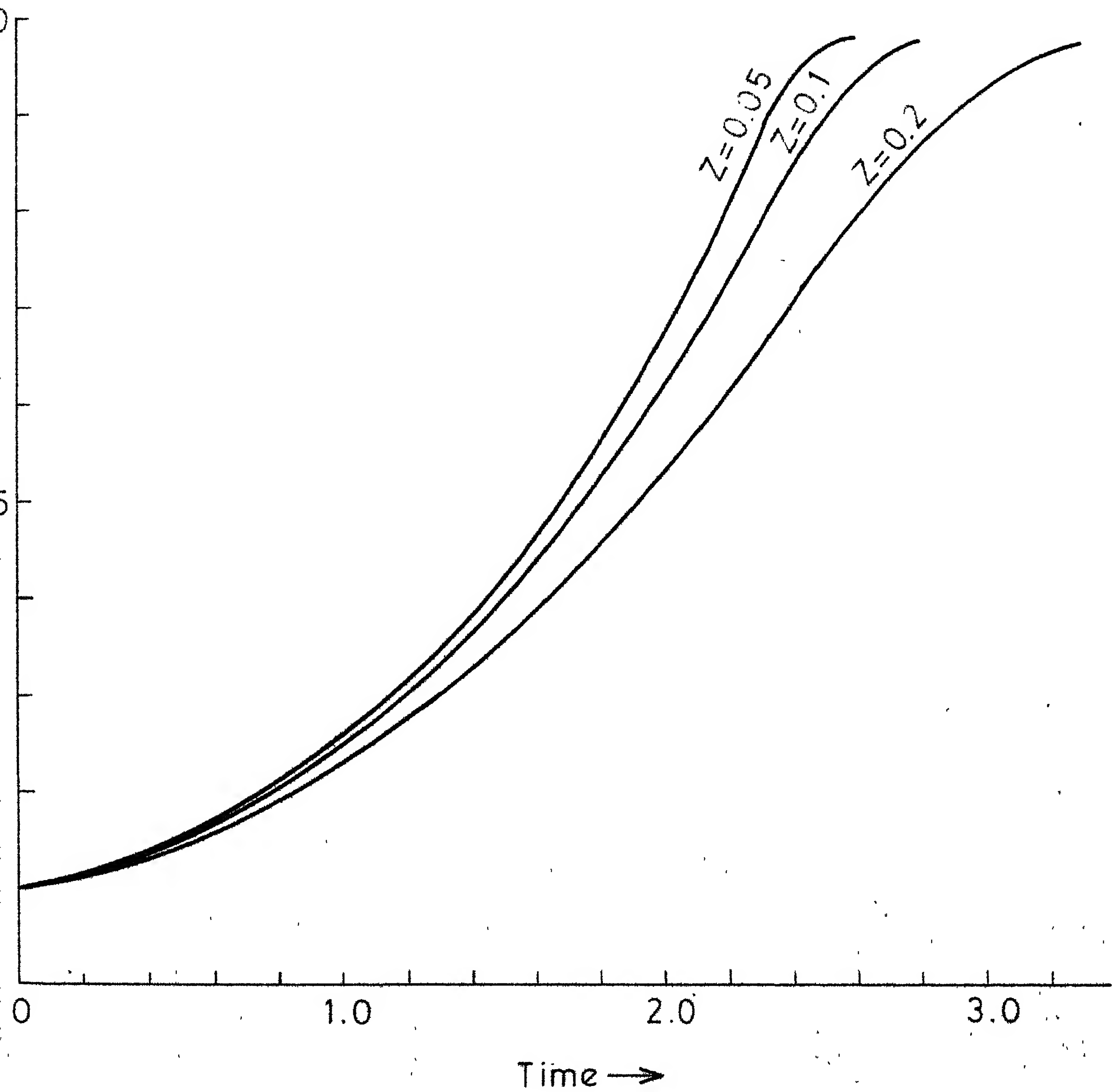


Fig. 2.12

population sizes. Consider the model

$$\frac{dN}{dt} = g(N)\,[N-N_e] \tag{79}$$

It will have a point of inflexion if

$$\frac{d^2N}{dt^2} = [g(N) + g'(N)\,(N-N_e)]\frac{dN}{dt}=0 \tag{80}$$

is satisfied by KN_e, where $0 < K < 1$

We consider some special cases

(i) $g(N) = AN+B$

Equation (80) gives

$$AKN_e + B + A\,(KN_e - N_e) = 0$$

or $$AN_e(2K-1) + B = 0 \tag{81}$$

$B = 0$, $K = \frac{1}{2}$ satisfies it. This corresponds to the logistic law.

From (81)

$$K = \frac{1}{2} - \frac{B}{2AN_e}\,, \quad \frac{B}{A} = (1-2K)N_e \tag{82}$$

If $\left|\frac{B}{AN_e}\right| < 1$, then the point of inflexion occur before half the final population size is reached if B and A have the same sign and after this if B and A have opposite sign.

If we know N_e and K i.e. if we know the final population size and the position of the point of inflexion, then

$$\frac{dN}{dt} = A[N+N_e(1-2K)]\,[N-N_e] \tag{83}$$

gives the simplest such model

(ii) $$g(N) = AN^2 + BN + C \tag{84}$$

Equation (80) gives

$$AK^2N_e^2+BKN_e+C + (2AKN_e+B)\ (KN_e-N_e) = 0 \tag{85}$$

and we can choose any value of A,B,C to satisfy (85)

(iii) Similarly we can take $g(N)$ is a polynomial of any degree or a rational function where denominator does not vanish between 0 and 1

(iv) If $g(N) = Ae^{aN}$, we get (86)

$$1+aN_e(K-1) = 0 \quad \text{or} \quad a = \frac{1}{(1-K)N_e} \tag{87}$$

Thus

$$\frac{dN}{dt} = A \exp\left[\frac{1}{(1-K)N_e}\right]\left[N-N_e\right] \tag{88}$$

gives a growth curve with limiting population size N_e and the point of inflexion at KN_e.

We can thus get a large variety of models with points of inflexion and limiting population sizes. Even any data showing these features, we can choose the model to give an optimum fit.

CHAPTER - 3

DIFFERENCE EQUATION MODELS IN ECOLOGY AND EPIDEMICS

3.1 INTRODUCTION

Mathematical ecology and epidemology are among the most fascinating areas of study today. Growth and decay of populations, effects of pollution on population growth, prey-predator and host-parasite models, competition between species, spread of epidemics and rumours all provide fascinating applications of mathematics. Burghes [1975] demonstrated how population dynamics can be used to motivate the study of differential equations at the undergraduate level. Kapur [1978, 1979] showed how problems of biomathematics can be used to motivate the study of partial differential equations, matrix theory, stability theory, stochastic processes, statistical mechanics, optimization techniques etc. because these and other sophisticated techniques are needed to solve hundreds of challenging problems which remain unsolved in these fields.

Differential equation models are accessible to only those who have had a first course on differential and integral calculus and numerical analysis. On the other hand difference equation or recurrence relation models are accessible immediately after a first course on elementary algebra and a few lectures on computer programming.

Both these types of models have been used in the literature and both can represent reality. In fact the validity of a model can only be tested by comparing its predictions with actual observations. Moreover differential equations are usually obtained by first writing difference equations and then using a limiting process. For numerical integration, we have again to transform the differential equations to difference equations.

In our discussions we shall not even require the theory of difference equations. Given a recurrence relation

$$u_n = a\, u_{n-1} + b, \tag{1}$$

and given a, b, u_0, we should be able to find successively $u_1, u_2, u_3, \ldots$. Similarly given the recurrence relations

$$\begin{aligned} u_n &= a_1 u_{n-1} + a_2 v_{n-1} + a_3 w_{n-1} + a_4 \\ v_n &= b_1 u_{n-1} + b_2 v_{n-1} + b_3 w_{n-1} + b_4 \\ w_n &= c_1 u_{n-1} + c_2 v_{n-1} + c_3 w_{n-1} + c_4 \end{aligned} \tag{2}$$

and given a_i, b_i, c_i $(i = 1,2,3,4)$, u_o, v_o, w_o, we should be able to find out successively

$$(u_1, v_1, w_1),\ (u_2, v_2, w_2),\ (u_3, v_3, w_3) \tag{3}$$

with such simple equipment, we can get deep insight into some of the important problems of ecology, epidemology, economics, sociology, operations research etc.

3.2 DIFFERENCE EQUATION MODELS

In recent years there has been an increased interest in modelling ecosystems with difference equations, renewing an approach dating back to Nicholson and Bailey [1935]. This interest stems from the recognition that many species have important discrete components in their life histories, such as synchronized breeding seasons and seasonal deaths.

Difference equation models are more or less analogous to the more common differential equation models. Single species logistic models of various forms have been investigated by Maynard Smith [1968], Pielou [1969], Cook [1971], May [1974, 1975] and others. Parasite-host interactions, the original topic of the Nicholson-Bailey investigation, have been considered by Maynard Smith [1968, 1974], Hassel and Varley [1969] and, with extensions of spatial variation by Allen [1975]. Predator-prey systems have been studied by Maynard smith [1968], Maynard Smith and Slatkin [1973], Beddington et al [1975], and others. Fretwell [1972] modelled species dynamics in seasonal environments by using difference equations Rolf Heller [1978] used difference equations for two prey-predator considering delayed population growth and starvation. He examined how the different assumptions can alter the dynamic behaviour of prey-predator model. Adi Raveh and Uzi Ritte [1976] used difference equations for simulating frequency dependent changes in gene frequencies. Donald L. DE Angels [1976] compared birth and death model and a stochastic

difference equation model, using data for a giant Canada-goose population. PHIL Diamond [1976] used difference equation for estimating domains of non-global asymptotic stability and region of resilance for biological systems. Masao Nakumura [1973] show that a certain limiting property of a system of linear homogeneous difference equations is characterized by a solution to a nonlinear system. Linear difference equations have been applied in estimation and prediction by Poole [1972] and in age distribution models by Leslie [1945].

The behaviour of difference equations in the neighbourhood of equilibria is known to be more complex than that of corresponding differential equation models used in describing continuous systems. The choice between continuous and discrete population models from the point of view of stability has been discussed by a number of authors including Driessche [1974], Duffin [1969], Innes [1974], May [1973a, 1973b] and Usher [1969]. It has been shown that the stability of discrete model represented by a system of difference equations, which is analogous to a continuous model represented by a system of differential equations, depends on the operator used.

May [1973b] shows that difference equations tend to be less stable than their differential equation twins, because the finite time lapse between generations of growth will have the destabilizing effects associated with any time lag

interacting system. His discussion makes it explicit, clearly stability of the difference equations system implies stability of the differential equation one, but the converse is not necessarily true. Priesche [1974] using a particular operational rule has shown that the resulting analogous discrete system is as stable as the differential equation system. We shall obtain in the next chapter a class of operators for which the difference equation system is mor stable than the corresponding differential equation system.

3.3 GROWTH OF A POPULATION

We assume that the births and deaths in a unit interval of time are proportional to the population size at the beginning of this interval so that if $X(t)$ is the population at time t, we get

$$X(t+1) - X(t) = BX(t) - DX(t) = aX(t) \qquad (4)$$

or

$$X(t+1) = (1+a)\,X(t)$$

Given $X(0)$, we easily find that

$$X(1) = (1+a)X(0),\ X(2) = (1+a)^2\,X(0), \ldots, X(t) = (1+a)^t X(0) \qquad (5)$$

The graph of $X(t)/X(0)$ is given in figure 3.1 for $a = .10$, $.15$ and $.25$.

It may be noted that the unit interval in the above discussion can, in practice, be chosen as small as we like

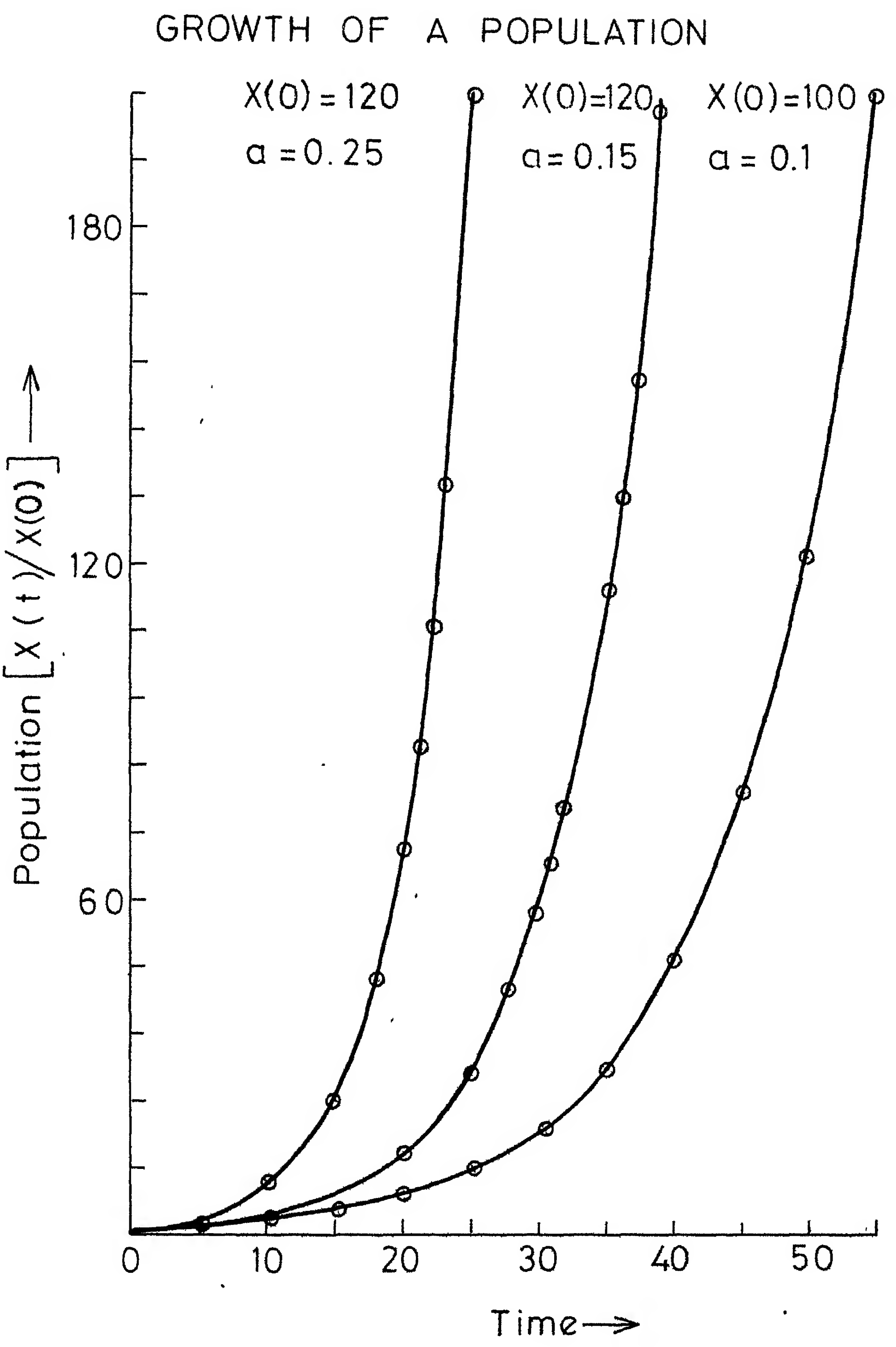

GROWTH OF A POPULATION
X(0) = 120
a = 0.25
X(0)=120
a = 0.15
X(0)=100
a = 0.1
180
120
60
Population [X(t)/X(0)] →
0
10
20
30
40
50
Time →

Fig. 3.1

by choosing the time-scale appropriately. Thus we may take unit interval of time as a year, a month, a day, an hour, a minute, a second or even a microsecond depending on the population and the accuracy required.

The smaller the unit interval chosen, the nearer will be the solution of the difference equation model to that of the corresponding differential equation model, but at the same time, the number of calculations required will also be larger. The unit time interval chosen thus may also depend on the computing device available which may be unaided mental calculations or logarithmic tables or slide rule or pocket calculator as on analogue computer or a digital computer.

In the present case, we may note that the corresponding difference and differential equation models are

$$X(t+1) - X(t) = aX(t), \quad \frac{dX}{dt} = a'X(t)$$

and their solutions are

$$X(t) = (1+a)^t X(0), \quad X(t) = e^{a't} X(0)$$

The two solutions are identical if

$$e^{a'} = (1+a).$$

3.4 GROWTH OF A POPULATION WITH LIMITED RESOURCES

Due to interval competition for limited resources, the increment in population size in a unit time interval is reduced

by an amount proportional to the square of the population size at the beginning of the time interval. If there are $X(t)$ individuals, each competes for resources against everyone and as such the term due to competition depends on $X^2(t)$. Our model becomes

$$X(t+1) - X(t) = aX(t) - bX^2(t) = X(t)[a-bX(t)] \quad (6)$$

Given $X(0)$, a,b we can successively find $X(1)$, $X(2)$, $X(3),\ldots,X(t),\ldots$. The graphs of $X(t)$ for the following values of $X(0)$, a,b* are shown in Figure 3.2

(i) $X(0) = 30.0$, $a = .04$, $b = .0001$

(ii) $X(0) = 10.0$, $a = .02$, $b = .0001$

(iii) $X(0) = 5.0$, $a = .09$, $b = .001$

It appears that the growth curves are all S-shaped and as t increases, $X(t)$ approaches the value a/b. This can also be seen from (6) since when $X(t)$ is very near to a/b, the increment in $X(t)$ is very small.

We can draw the graphs for other values of $X(0)$, a and b. If $X(0)$ is greater than a/b, the curve approaches the line $X = a/b$ asymptotically from above.

Sometimes the equation (6) is replaced by

$$X(t+1) = CX(t)/1+dX(t) \quad (7)$$

It can easily be verified that the graph of (7) is also S-shaped. As $t \to \infty$,

* See Note 1 of Appendix

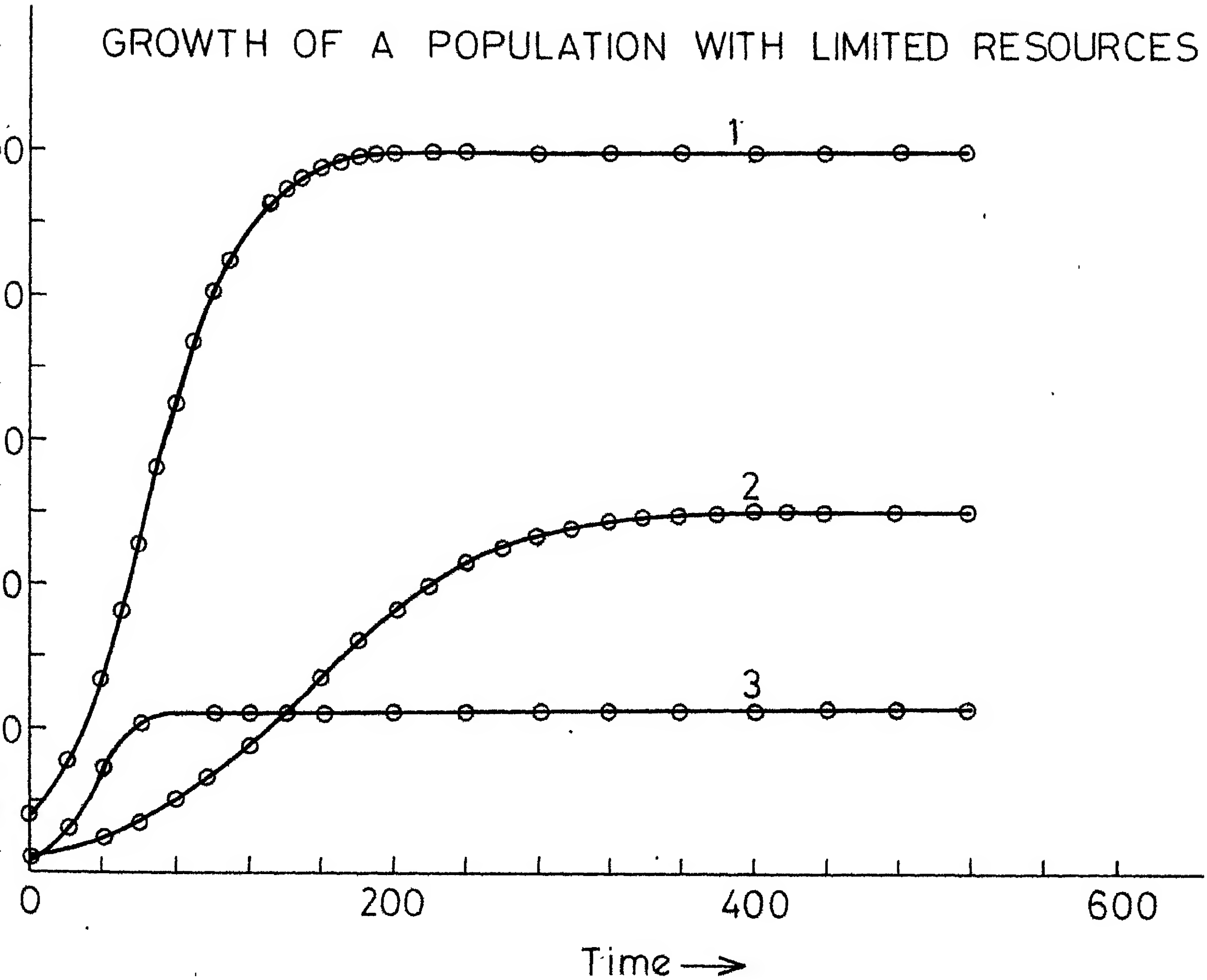

GROWTH OF A POPULATION WITH LIMITED RESOURCES
1
2
3
0
200
400
600
Time →

Fig. 3.2

$$X(t) \to (c-1)/d \tag{8}$$

In fact it can be verified by direct substitution that (7) has the exact solution

$$X(t) = \frac{(c-1)\,X_0}{dX_0 + (c-1-dX_0)c^{-t}} \quad \text{when } c \neq 1 \tag{9}^*$$

$$X_0/1+dX_0t \quad \text{when } c = 1$$

which is a solution of a differential equation of the form

$$\frac{dX}{dt} = aX - bX^2 \tag{10}$$

3.5 INFLUENCE OF POLLUTION ON POPULATION GROWTH

Pollution is a cumulative phenomena and depends on population growth. Pollution effect on population at time t depends in the populations at time t, at time t-1, at time t-2, and so on. Of course the pollution effect on population at time t of population at time t-T will decrease with T. We may take it to be a decreasing function K(T) of T.

We consider the model

$$X(t+1)-X(t) = aX(t)-bX^2(t)-cX(t)\left[X(0)K(t)+X(1)K(t-1) + \cdots + X(t)K(0)\right] \tag{11}$$

Given a, b, c, K(t), X(0), we can find successively X(1), X(2), X(3), ... Fig. 3.3 gives the graphs when $K(t) = e^{-t}$ and

$$X(0) = 30.0, \quad a = 0.04, \quad b = 0.0001$$

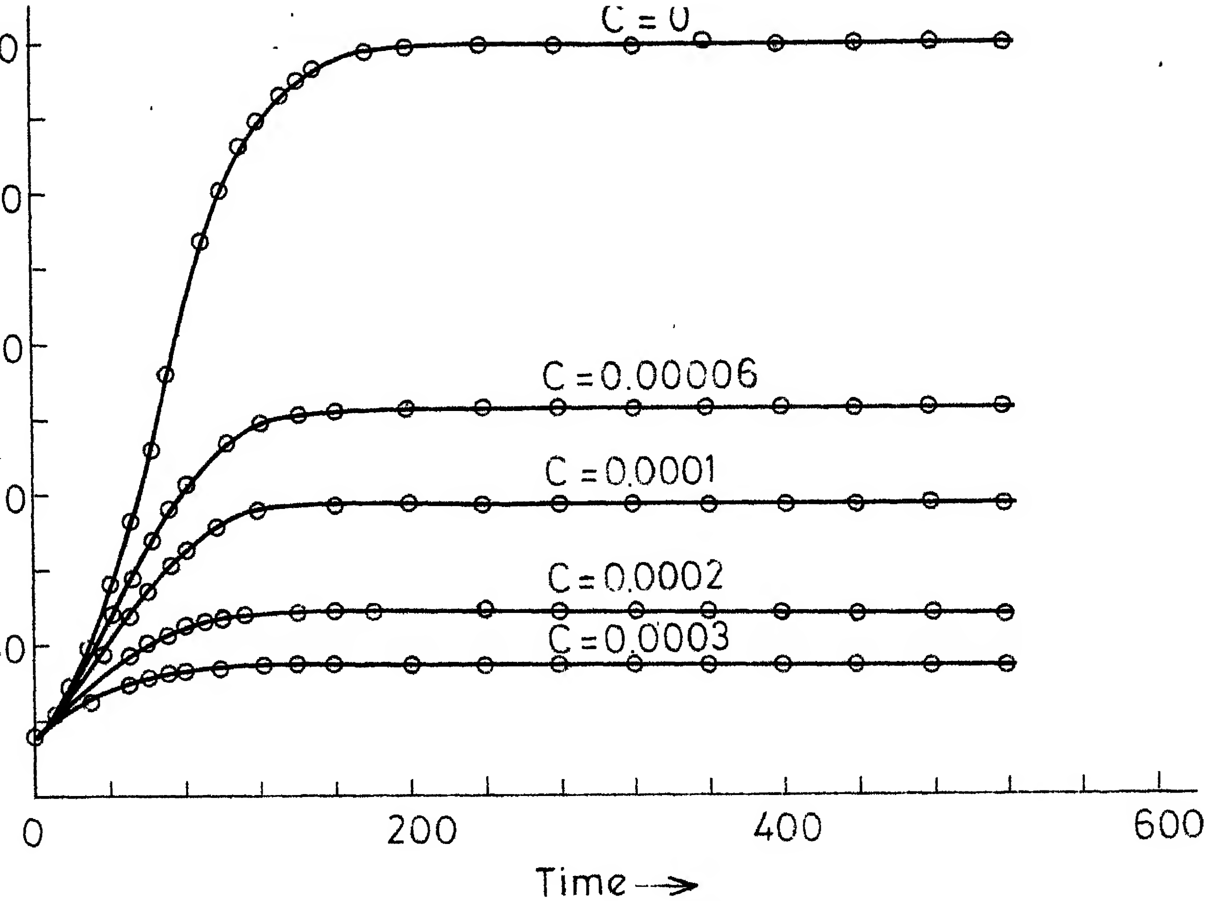
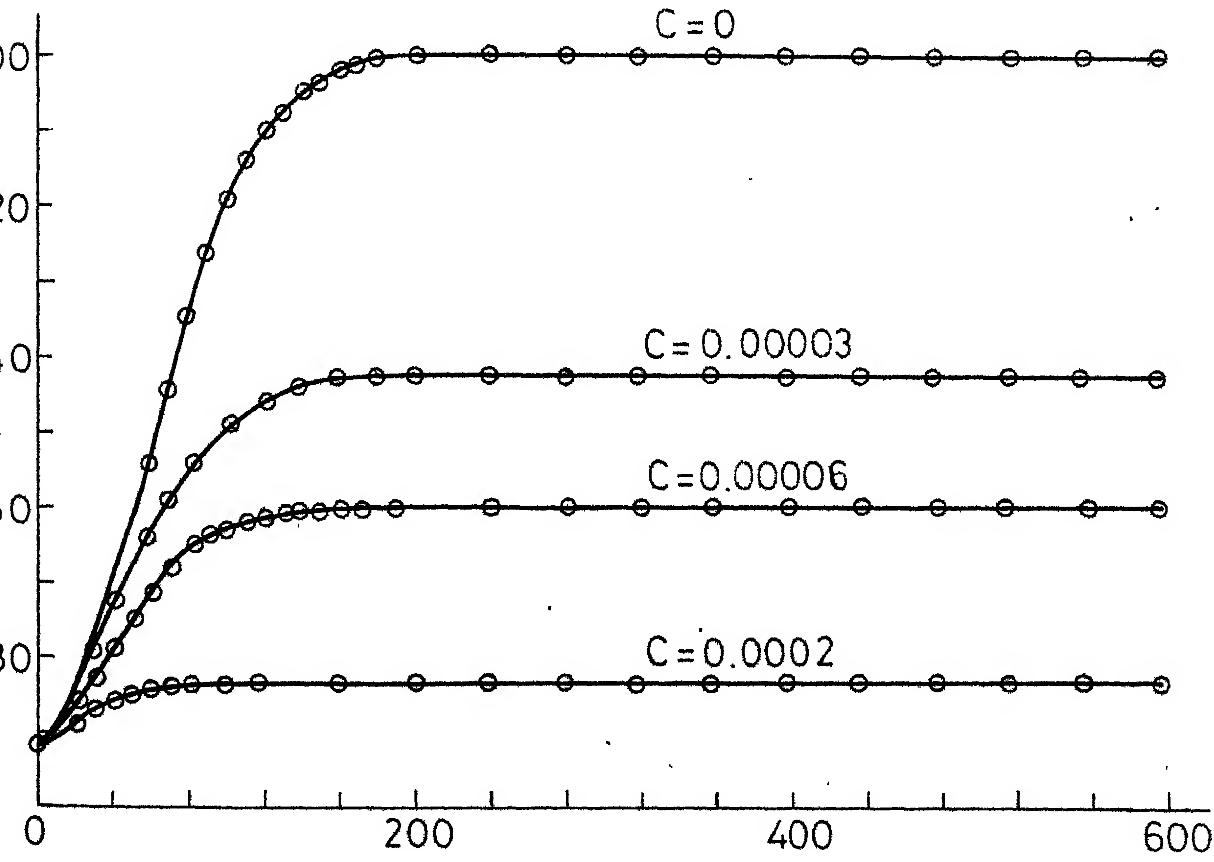

C = 0
C = 0.00006
C = 0.0001
C = 0.0002
C = 0.0003
0
200
400
600
Time →

Fig 3.3


C = 0
C = 0.00003
C = 0.00006
C = 0.0002
0
200
400
600

and c takes the values

$$c = 0.00006,\ 0.00001,\ 0.0002,\ 0.0003$$

We note that as c increases, the population decreases. This is expected since increase of pollution should lead to decrease of population. We also find as $t \to \infty$, $X(t) \to$ a finite limit which is verified to be

$$\frac{a}{b+c\,\frac{e}{(e-1)}} = \frac{a}{b+1.58c} \tag{12}$$

We also note that the time taken to reach this value is almost independent of c.

We may also take $K(t)$ as a linear function of t i.e.

$$K(T) = 1-T/n, \quad T < n; \ K(T) = 0, \ T = n \tag{13}$$

so that

$$X(t+1)-X(t) = aX(t)-bX^2(t)-cX(t)\Big[X(t)+(1-\tfrac{1}{n})\,X(t-1)+(1-\tfrac{2}{n})X(t-2)+\ldots.+(1-\tfrac{n}{n})\,X(t-n)\Big] \tag{14}$$

In this case, we should be given $a, b, c, X(0), X(1), \ldots, X(n-1)$ and equation (14) should be applied when $t=n, n+1, n+2, \ldots$ Figure 3.4 illustrates the case when $n = 4$ and where $a, b, c, X(0), X(1), X(2), X(3)$ have same values as in Figure 3.3. Here

$$X(t) \to \frac{a}{b+2.5c} \quad \text{as} \quad t \to \infty \tag{15}$$

For the general value of n,

$$X(t) \to \frac{a}{b+\frac{1}{2}(n+1)c} \quad \text{as} \quad t \to \infty \tag{16}$$

In model (11), we assumed that the pollution before an arbitrary origin of time does not affect the future population. This can only be true if there was no pollution before this time. We can also assume that it is only populations at n times viz. t, t-1, t-2,... t-(n-1) which affect the population at time t so that we may consider the model

$$X(t+1)-X(t) = aX(t)-bX^2(t)-cX(t)\left[1\ X(t)+e^{-t}X(t-1)+\dots +e^{-(n-1)t}(t-\overline{n-1})\right] \tag{17}$$

In this case we should be given a, b, c, X(0), X(1),..., X(n-1). It is easily seen that

$$\underset{t \to \infty}{\mathrm{Lt}}\ X(t) = \frac{a}{b+c(1-e^{-n})/(1-e^{-1})} \tag{18}$$

we may note that in this case it is not possible to write the analytical solution of (11), (14), (17) or the corresponding differential equation model

$$\frac{dX}{dt} = aX-bX^2-cX\int_{t-T_0}^{t} K(T)\ X(t-T)\,dT \tag{19}$$

where T_0 is the total time for which the effect of pollution is effective. For special values of K(T) (e.g. when K(T)=1) analytical solutions however do exist.

The difference equation recurrence-relation approach can however always be used to get insight into the influence of pollution.

3.6 INFLUENCE OF AGE STRUCTURE

For this Burghes [1975] obtained the time-lag differential equations

$$\frac{dX}{dt} = \theta\ [\alpha - \gamma X(t-T)]\ X(t-T) - BX(t) \qquad (20)$$

For discussing its behaviour, he however used the difference equation

$$X(t+1) - X(t) = \theta[\alpha - \gamma X(t-T)]\ X(t-T) - BX(t) \qquad (21)$$

and he drew the corresponding graph for $T = 30$, $X_0 = 5$ and

$$B = 0.05,\ \theta\alpha = 0.25,\ \theta\gamma = 0.01,\ B = 0.05,\ \theta\alpha = 0.025, \theta\gamma = 0.02$$
$$B = 0.10,\ \theta\alpha = 0.25,\ \theta\gamma = 0.01;\ B = 0.15,\ \theta\alpha = 0.25,\ \theta\gamma = 0.01 \qquad (22)$$

To solve (21), we have either to specify the values of $X(0), X(1), \ldots, X(30)$ or we can assume as Burghes did that upto $t = 30$, only deaths takes place so that (21) is replaced by

$$X(t+1) - X(t) = BX(t),\ (t=0,1,2,\ldots,29) \qquad (23)$$

The example illustrates how difference equations approach can be used to get insight into phenomena normally represented by delay differential equations.

3.7 AN ALTERNATIVE METHOD OF TAKING AGE STRUCTURE INTO ACCOUNT

We can divide the population into three groups

(i) ~~Pre-~~reproductive children (ii) Pre-reproductive adults

(iii) Post-reproductive old persons

Let $X_1(t)$, $X_2(t)$, $X_3(t)$ be the populations of the three groups at time t, then

$$\begin{aligned} X_1(t+1) - X_1(t) &= a_1X_2(t) - b_1X_1(t) \\ X_2(t+1) - X_2(t) &= a_2X_1(t) - b_2X_2(t) \\ X_3(t+1) - X_3(t) &= a_3X_2(t) - b_3X_3(t) \end{aligned} \tag{24}$$

In (24), the first term on the R.H.S. of the first equation represents number of births of children per unit time and this is proportional to the size of the adult group, and the second term represents deaths and migrations per unit time which are proportional to the size of the population of the children. In the same way $a_2X_2(t)$ and $a_3X_3(t)$ represent migrations per unit time from the first group to the second and from the second to the third group and $b_2X_2(t)$ and $b_3X_3(t)$ represents deaths and migrations per unit time from the second and third groups respectively.

Given $X_1(0)$, $X_2(0)$, $X_3(0)$ we can proceed step by step to find $X_1(t)$, $X_2(t)$, $X_3(t)$.

We can write (24) in the form

$$X(t+1) = AX(t) \tag{25}$$

where

$$X(t) = \begin{bmatrix} X_1(t) \\ X_2(t) \\ X_3(t) \end{bmatrix} \qquad A = \begin{bmatrix} 1-b_1 & a_1 & 0 \\ a_2 & 1-b_2 & 0 \\ 0 & a_3 & 1-b_3 \end{bmatrix} \tag{26}$$

so that

$$X(t) = A^t X(0) \tag{27}$$

The eigenvalues of A are

$$\lambda_1,\ \lambda_2 = \frac{1}{2}\left[2-b_1-b_2 \pm \sqrt{(b_1-b_2)^2 + 4a_1a_2}\right],\ \lambda_3 = 1-b_3 \tag{28}$$

so that two of the eigenvalues are definitely less than unity and the third will be less than unity if $a_1a_2 < b_1b_2$. In this case the populations of the three groups will tend to zero as $t \to \infty$. If $a_1a_2 > b_1b_2$, population of each group increases exponentially. From (27)

$= C_{11}(\lambda_1)^n + C_{12}(\lambda_2)^n + C_{13}(\lambda_3)^n$, $i = 1, 2, 3$

$$X_1(t) = c_{11}e^{t \log \lambda_1} + c_{12}e^{t \log \lambda_2} + c_{13}e^{t \log \lambda_3}$$

$$X_2(t) = c_{21}e^{t \log \lambda_1} + c_{22}e^{t \log \lambda_2} + c_{23}e^{t \log \lambda_3}$$

$$X_3(t) = c_{31}e^{t \log \lambda_1} + c_{32}e^{t \log \lambda_2} + c_{33}e^{t \log \lambda_3} \tag{29}^*$$

If we can observe $X_1(t)$, $X_2(t)$, $X_3(t)$ over a period of time, we can use the method of exponential peeling to estimate the values of the parameters $a_1, a_2, a_3, b_1, b_2, b_3$.

Figures 3.5, 3.6, 3.7 give the growth curves for $X_1(t)$ $X_2(t)$, $X_3(t)$ when $X_1(0) = 100$, $X_2(0) = 100$, $X_3(0) = 100$ and in

FIG. 3.5.

(i) $a_1 = .05$, $a_2 = .02$, $b_1 = .03$, $b_2 = .02$, $a_3 = .02$, $b_3 = .05$

$$a_1 a_2 > b_1 b_2$$

FIG. 3.6

(ii) $a_1 = .04$, $a_2 = .03$, $b_1 = .03$, $b_2 = .04$, $a_3 = .02$, $b_3 = .05$

$$a_1 a_2 = b_1 b_2$$

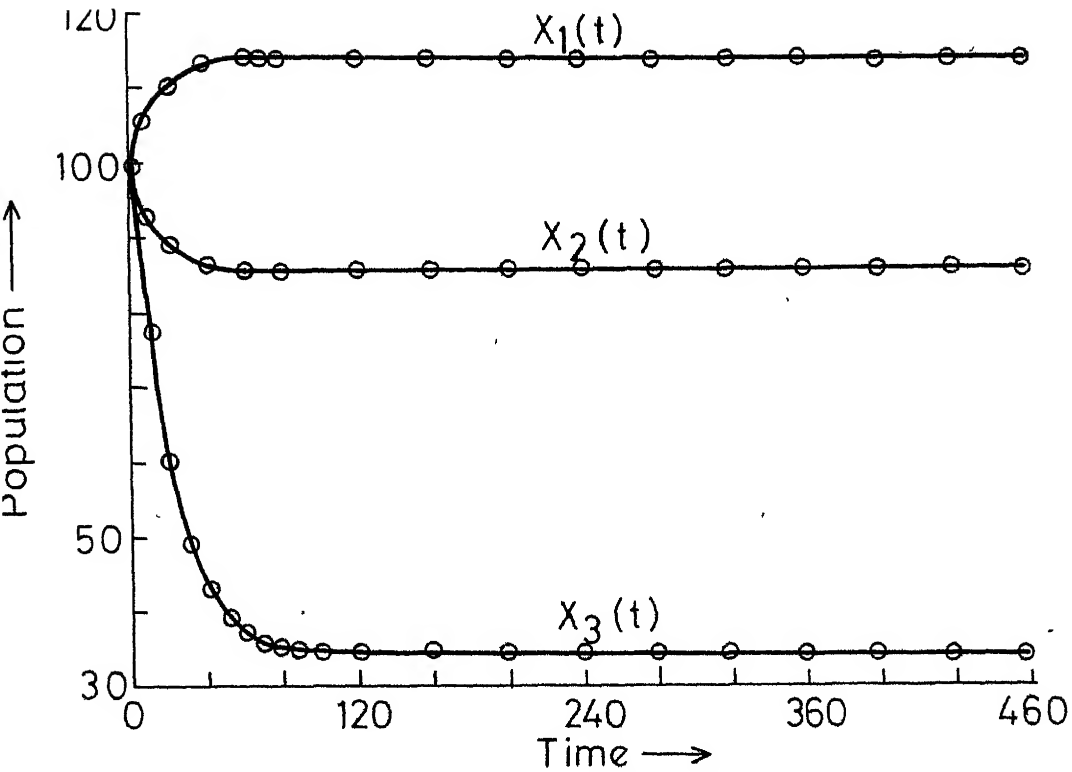
FIG. 3.7

(iii) $a_1 = .04$, $a_2 = .02$, $b_1 = .03$, $b_2 = .03$, $a_3 = .02$, $b_3 = .05$

$$a_1 a_2 < b_1 b_2$$

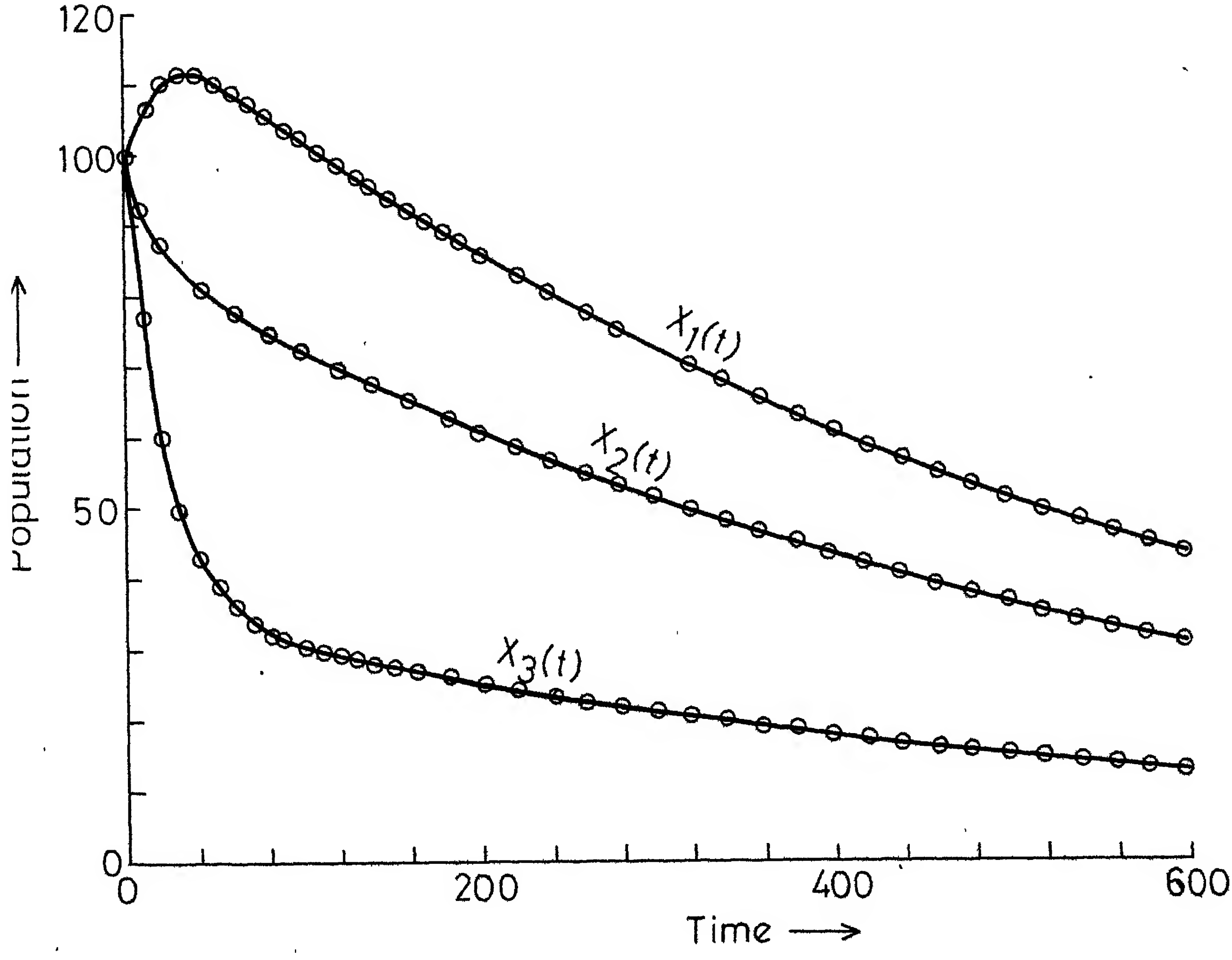
3.8 PREY-PREDATOR AND HOST-PARASITE MODELS

Let $X(t)$, $Y(t)$ be the populations of rats and cats at time t. Let us calculate the increments $X(t+1) - X(t)$ and $Y(t+1) - Y(t)$. In the absence of cats, population of rats increases and the increase is proportional to the size of this population, but due to the presence of cats, the rats population decreases and the decrease is assumed proportional to the product of the number of cats and rats. In the absence of rat , cats population decreases and the decrease is proportional to the number of cats and in the presence of rats, the cat population increases and the increase is proportional to the product of the number of rats and cats. This consideration gives



120
100
50
30
Population ⟶
$X_1(t)$
$X_2(t)$
$X_3(t)$
0
120
240
360
460
Time ⟶

Fig. 3.7



120
100
50
0
Population ⟶
$X_1(t)$
$X_2(t)$
$X_3(t)$
0
200
400
600
Time ⟶

Fig. 3.6

$$
\begin{aligned}
X(t+1) - X(t) &= a_1X(t) - b_1X(t)\,Y(t) \\
Y(t+1) - Y(t) &= -a_2Y(t) + b_2X(t)\,Y(t)
\end{aligned}
\qquad (30)
$$

Given $a_1, a_2, b_1, b_2, X(0), Y(0)$ we can calculate step by step $X(t)$, $Y(t)$ for any value of t. Figures 3.8, 3.9, 3.10 show the result of such a calculation for

$X(0) = 26,\ Y(0) = 7,$ * $a_1 = .01,\ a_2 = .02,\ b_1 = .002,\ b_2 = .001$
$X(0) = 25,\ Y(0) = 10$

The equilibrium point for which $X(t) = X(t+1)$, $Y(t) = Y(t+1)$ is

$X_e = 20, \quad Y_e = 5$ for Fig. 1

If the populations start at these values, they stay at these values.

The populations show periodic oscillations. In the phase space we do not get close trajectories as we get in the case of the corresponding differential equation model.

$$
\begin{aligned}
\frac{dX}{dt} &= a_1\,X(t) - b_1X(t)\,Y(t) \\
\frac{dY}{dt} &= -a_2\,Y(t) + b_2X(t)\,Y(t)
\end{aligned}
\qquad (31)
$$

However when the unit interval is small, the trajectories are almost closed. Moreover observations of natural populations also do not give close trajectories.

Here we have not considered self interaction. If this is taken into account then the equation (31) will become

$$
\begin{aligned}
X(t+1) - X(t) &= a_1X(t) - c_1X^2(t) - b_1X(t)\,Y(t) \\
Y(t+1) - Y(t) &= -a_2Y(t) - c_2Y^2(t) + b_2X(t)\,Y(t)
\end{aligned}
\qquad (32)
$$

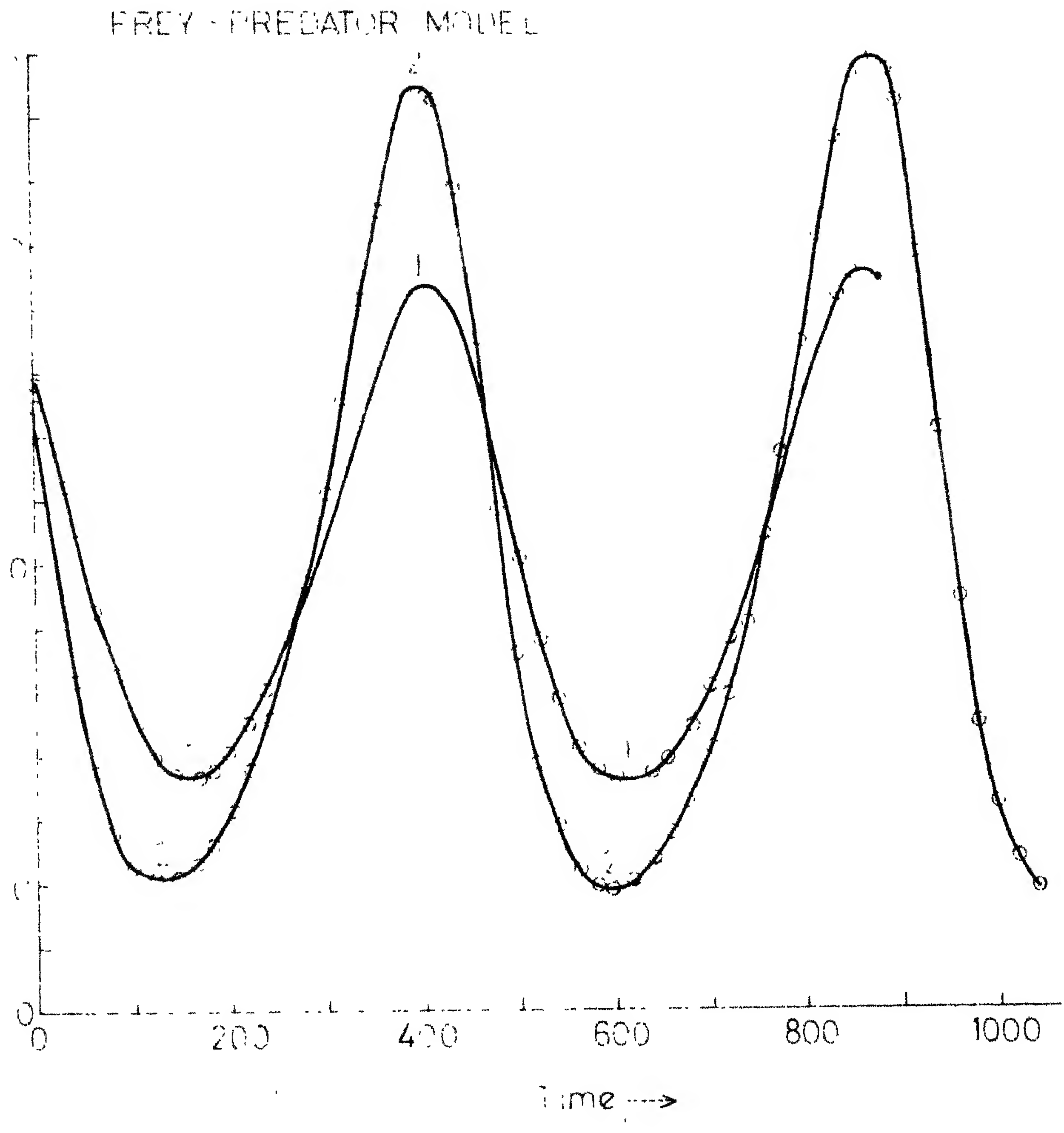


Fig 3 8

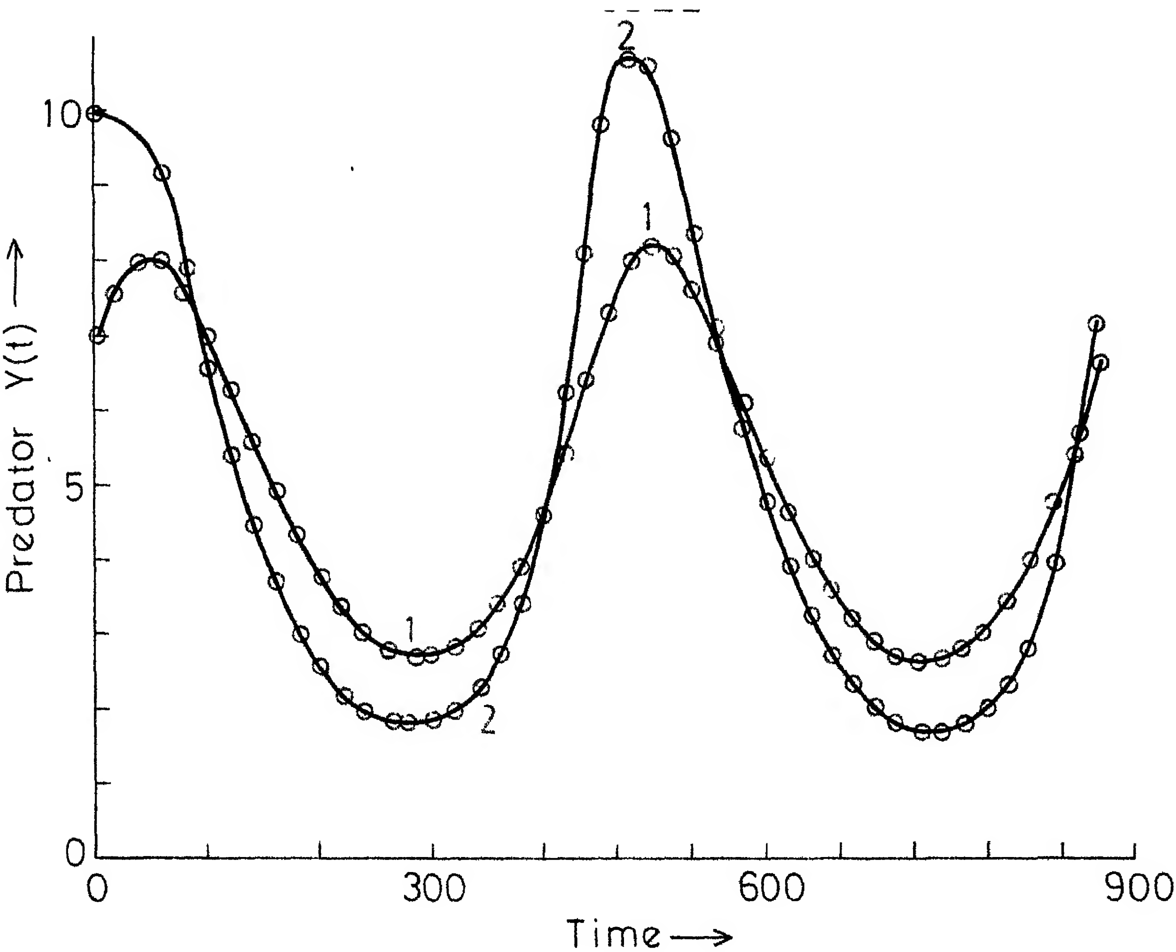


Fig. 3.9

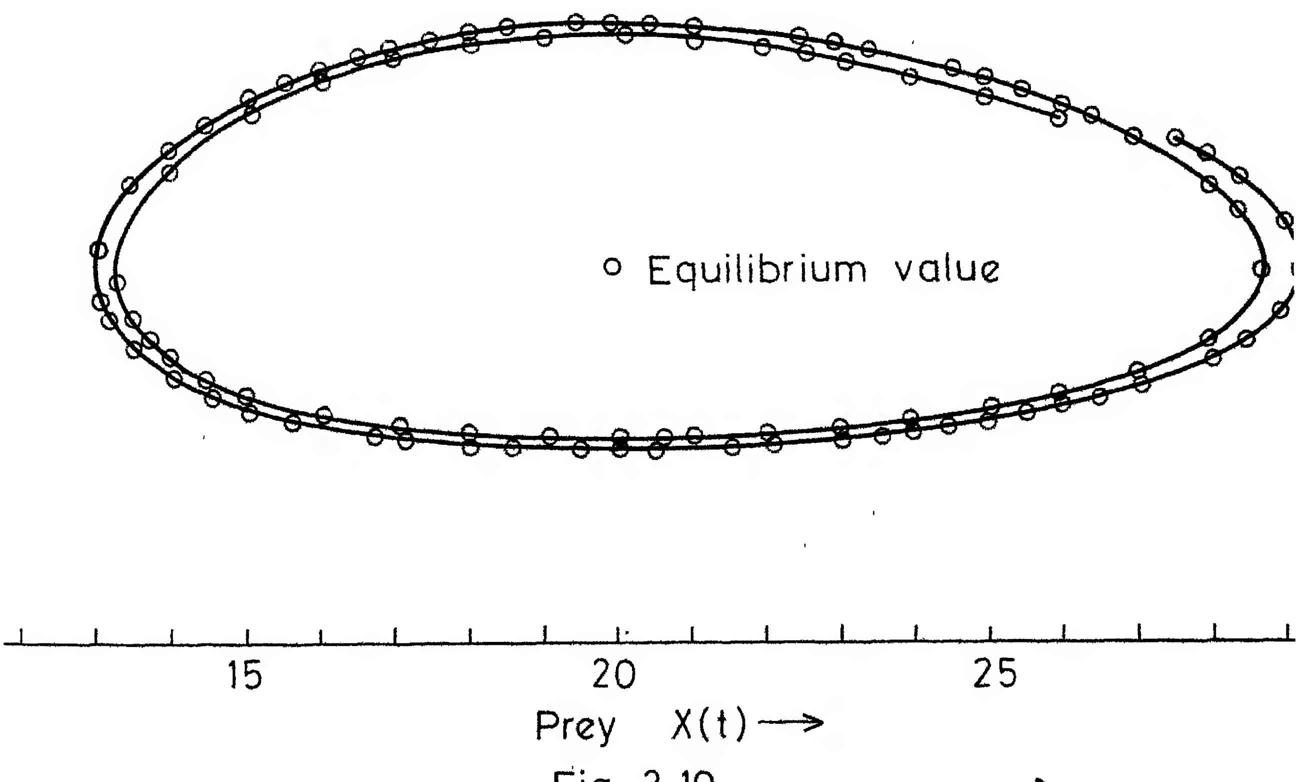


Fig. 3.10

Self interaction is harmful to growth for both populations. Behaviour in this situation for both prey and predater is shown in Figures 3.11, 3.12, 3.13

where

$a_1 = .01 \quad a_2 = .02$

$c_1 = .01 \quad c_2 = .02 \quad X(0) = 21.0$

$b_1 = .002 \quad b_2 = .001 \quad Y(0) = 6.0$

If there is a cover capable of protecting a limited number of prey, and of those prey unable to occupy this cover are killed, then all prey above some fixed number would be killed. It may also happen that the predator is rare, and limited by some factor other than the abundance of this particular prey. Each predator might than take a fixed quantity of prey regardless of the abundances of the prey. In this case a term X(0) is introduced in equation (31) which represents the number of prey those are not killed by predator. Model of this situation is given by

$$\begin{aligned} X(t+1) - X(t) &= aX(t) - bY(t)\,[X(t) - X(0)] \\ Y(t+1) - Y(t) &= -cY(t) + dY(t)\,[X(t) - X(0)] \end{aligned} \qquad (33)$$

population growth of prey and predator is shown in Figures 3.14, 3.15, 3.16

where in sub figures of Figures 3.14, 3.15, 3.16, we take

1	$a = .01$		2	$a = .01$
	$b = .002$			$b = .004$
	$c = .02$			$c = .03$
	$d = .001$			$d = .002$

3	a	=	.04		4	a	=	.08
	b	=	.02			b	=	.009
	c	=	.03			c	=	.05
	d	=	.002			d	=	.006

$X(0) = 21.0$ and $Y(0) = 6.0$ are common in all sub figures. Both predator-prey population oscillate with time. The behaviour of prey with respect to predator is shown in Figure 3.16. It shows that as time increases they tend to equolibrium value.

3.9 INTERACTION BETWEEN PREDATORS AND PREY

Let X_t are the number of prey and Y_t, Z_t are adult and young predators. In each interval, each predator must find and eat one prey. If it fails to find a prey it dies. If it succeeds it does not seek ~~for~~ a second prey until the next interval. The model of this type is

$$Y_{t+1} = Y_t \left[1-\exp\left(-\alpha X_t\right)\right]$$

$$Z_{t+1} = Z_t \left[1-\exp\left(-\beta X_t\right)\right] \tag{34}$$

$$X_{t+1} = X_t - Y_{t+1} - Z_{t+1}$$

Here α, and β are the effective search areas of adult and young respectively.

If we plot a graph between prey population and time, we see that prey population decreases exponentially and after some time it will become constant. The behaviour of adult

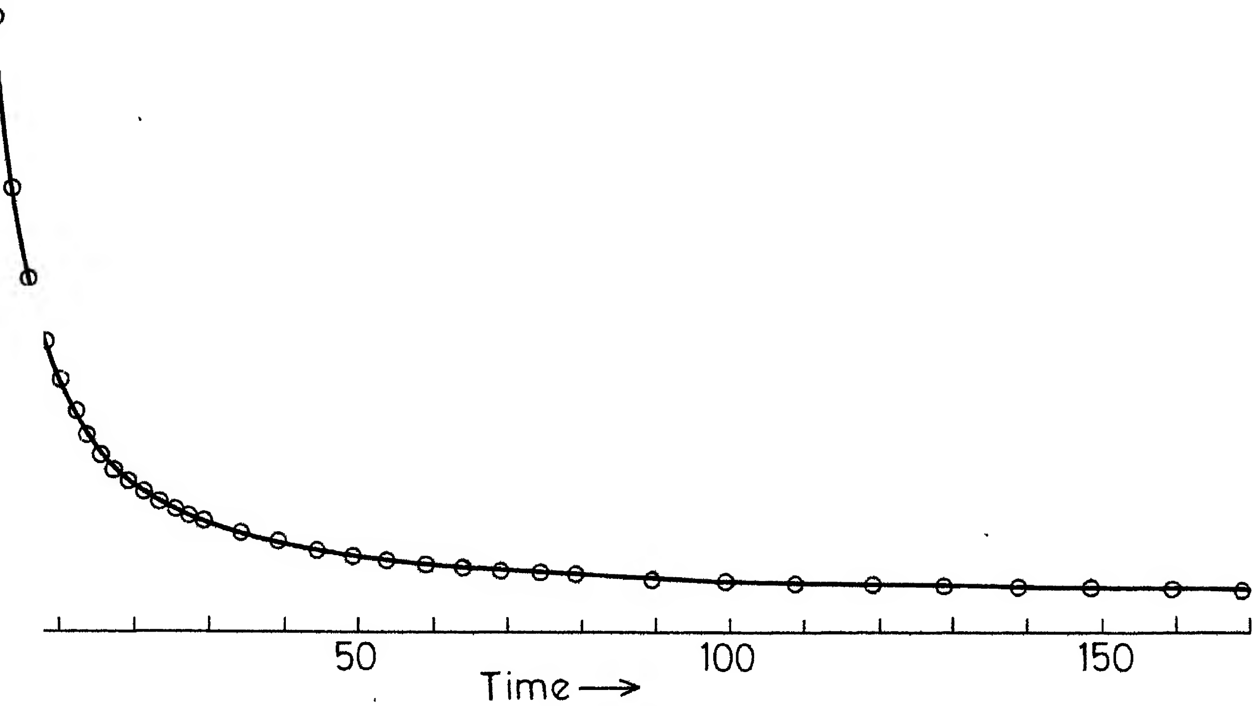


Fig. 3.11

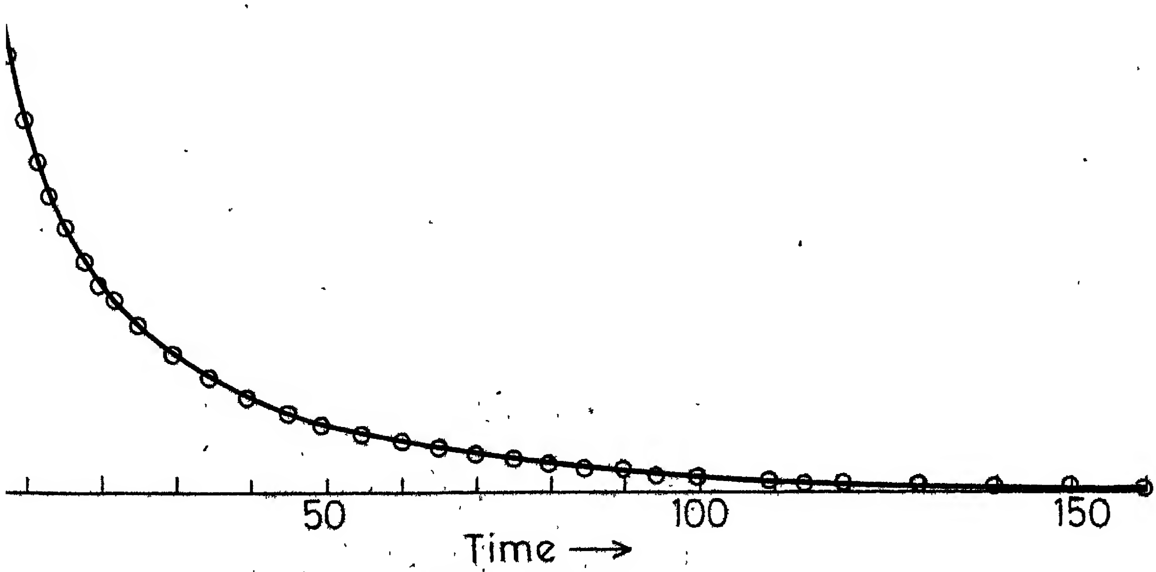


Fig. 3.12

PREY - PREDATOR WITH SELF INTERACTION

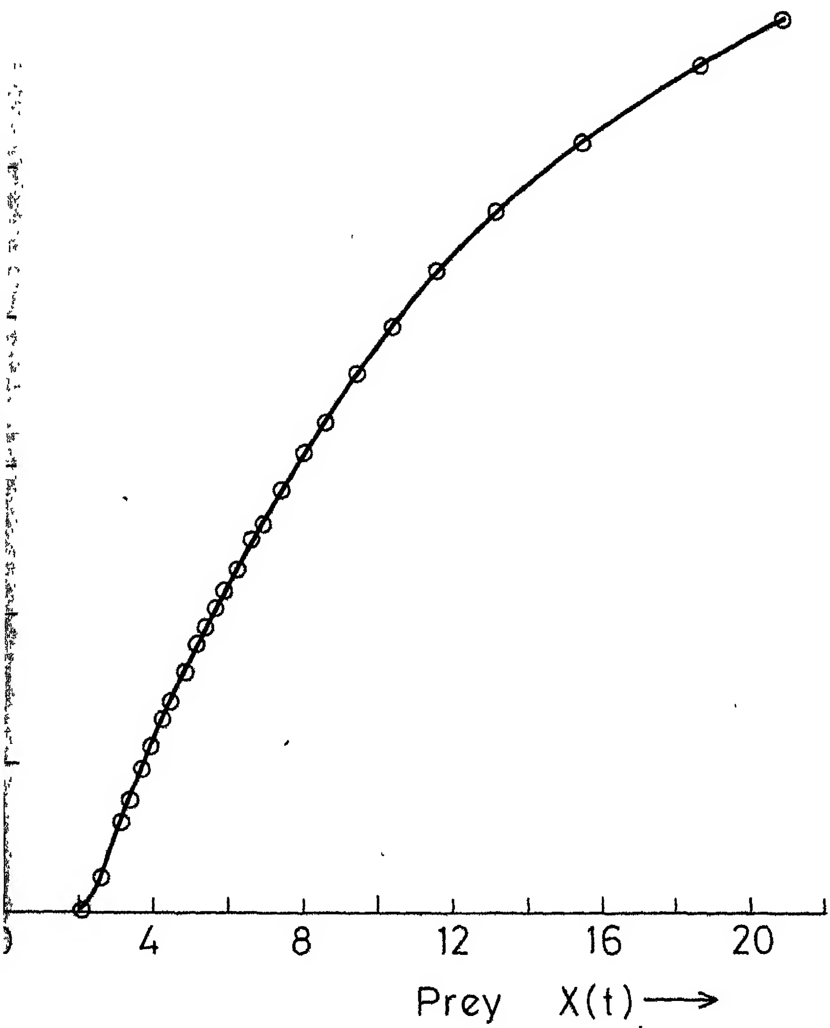


Fig. 3.13

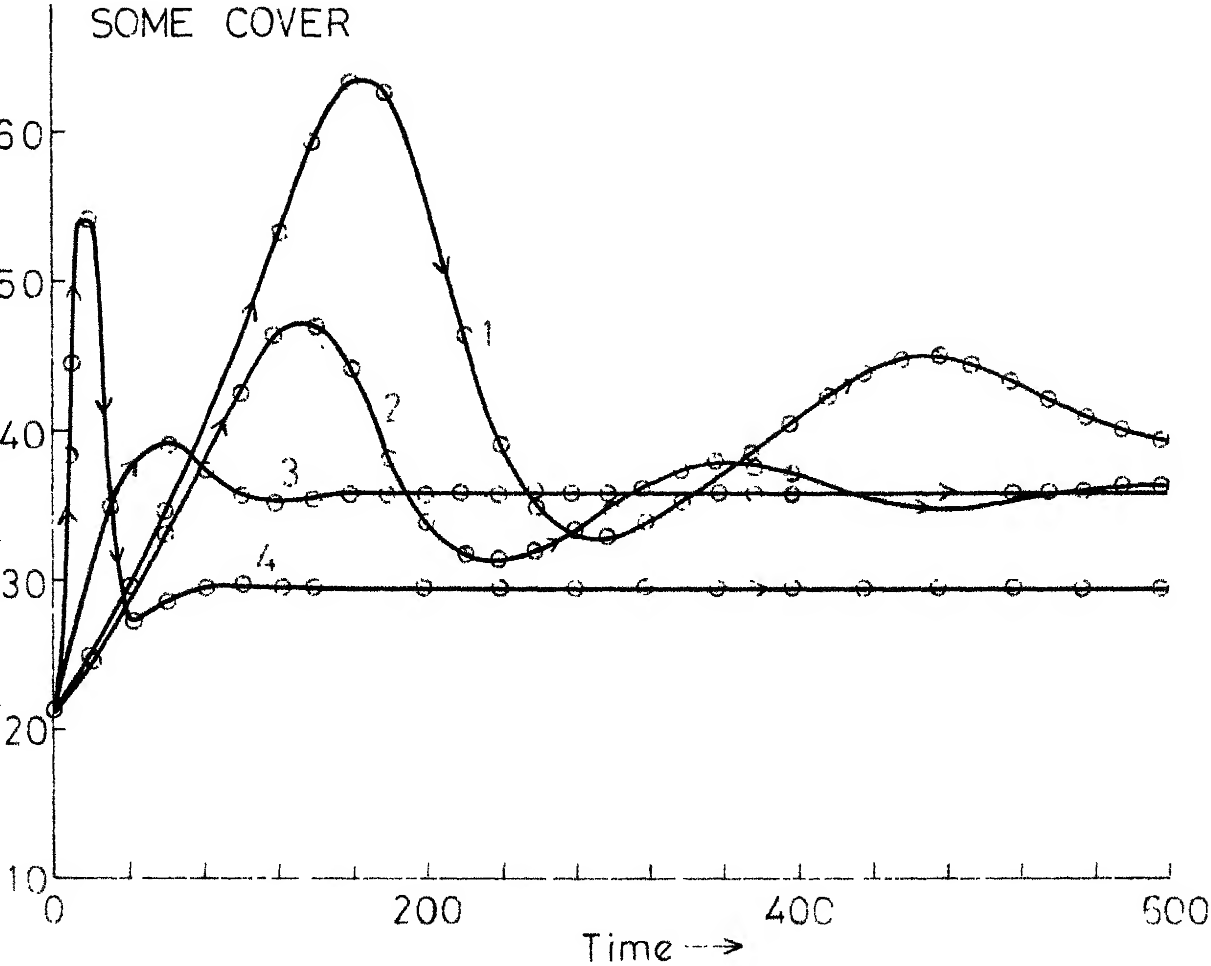
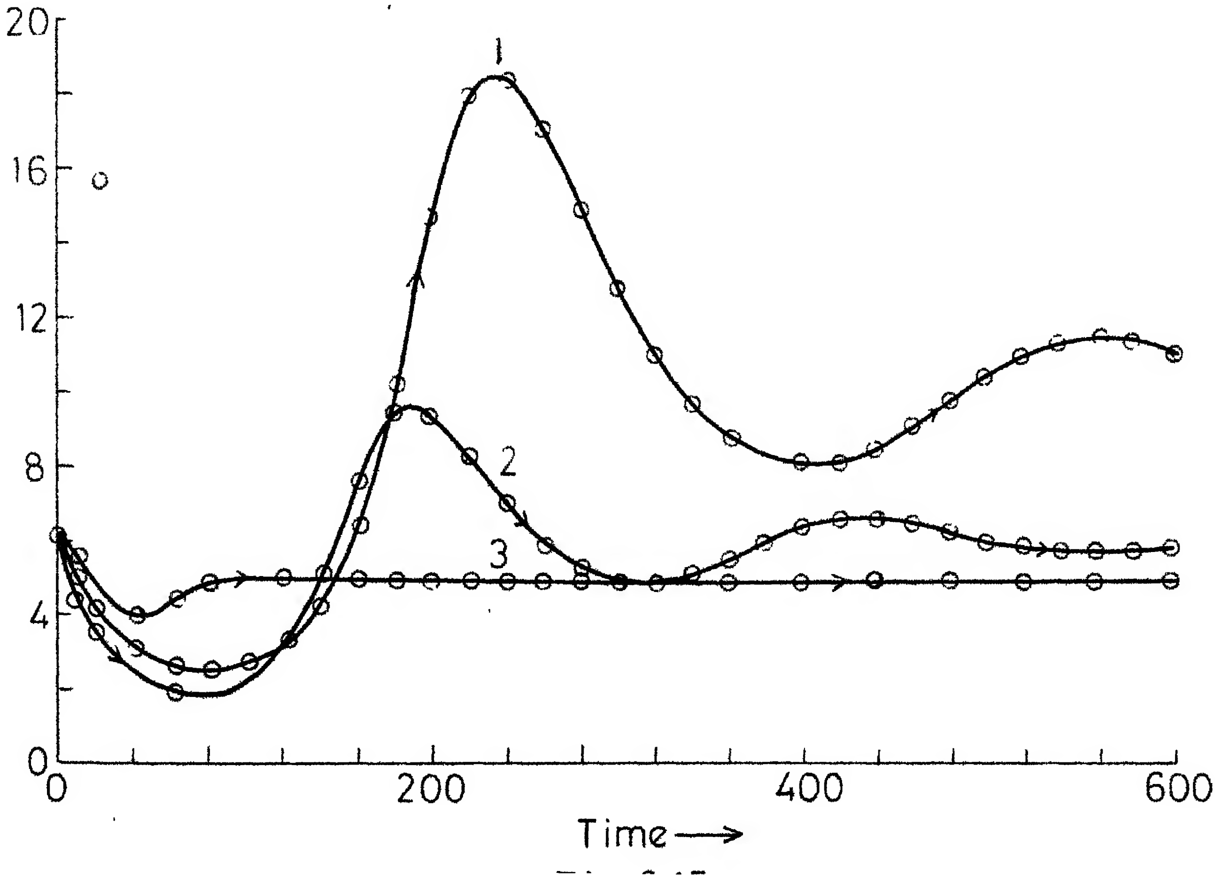

SOME COVER
60
50
40
30
20
10
0
200
400
600
Time
1
2
3
4

Fig 314


20
16
12
8
4
0
200
400
600
Time
1
2
3

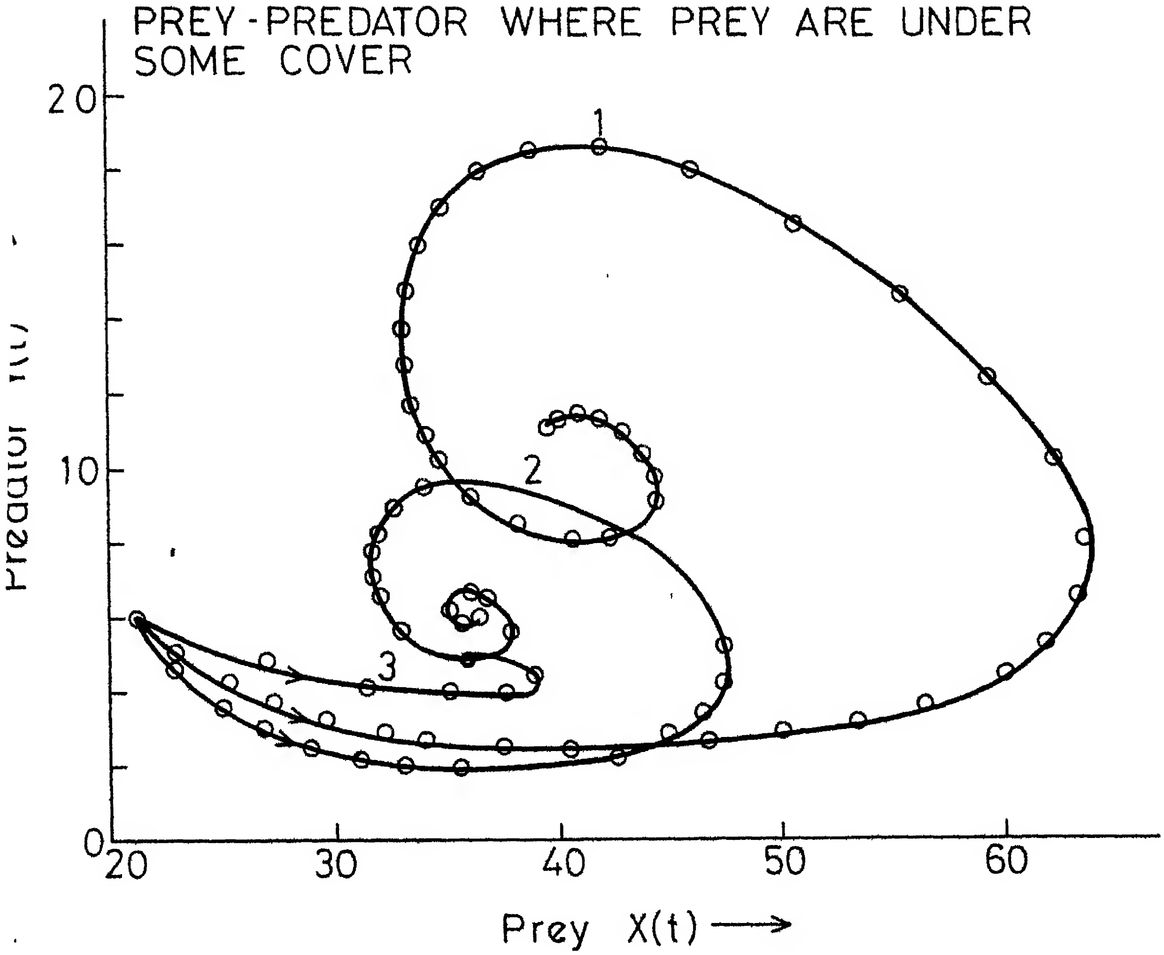

PREY-PREDATOR WHERE PREY ARE UNDER SOME COVER
20
10
0
1
2
3
20
30
40
50
60
Prey X(t)

Fig. 3.16

and young predators is similar. Both populations decrease exponentially and will die out ultimately. Behaviour of X_t, Y_t and Z_t is shown in

Fig. 3.17 Fig. 3.18 Fig. 3.19

The values of constants and initial values are

$\alpha = .006$ $X(0) = 400$

$Z(0) = 40$

$\beta = .004$ $Y(0) = 60$

3.10 LESLIE's EQUATIONS

$$\begin{aligned} X(t+1) - \dot{X}(t) &= aX(t) - bX^2(t) - cX(t)Y(t) \\ Y(t+1) - \dot{Y}(t) &= eY(t) - fY^2(t)/X(t) \end{aligned} \qquad (35)$$

This is the prey-predator equation with some modification. First equation is of prey and is the same as Voltera's equation with damping. Modification occurs in the second equation. If prey per predator i.e. X/Y is large then predator increases exponentially if X/Y = f/e then the predator is at equilibrium. If X/Y falls below f/e the predator will die out.

Behaviour of this equation for

$a = .01$ $c = .002$ $f = .01$

$Y(0) = 3.0$

$b = .02$ $e = .02$ $X(0) = 15.0$

is shown in Fig. 3.20 and Fig. 3.21 .

* See Note 5 of Appendix

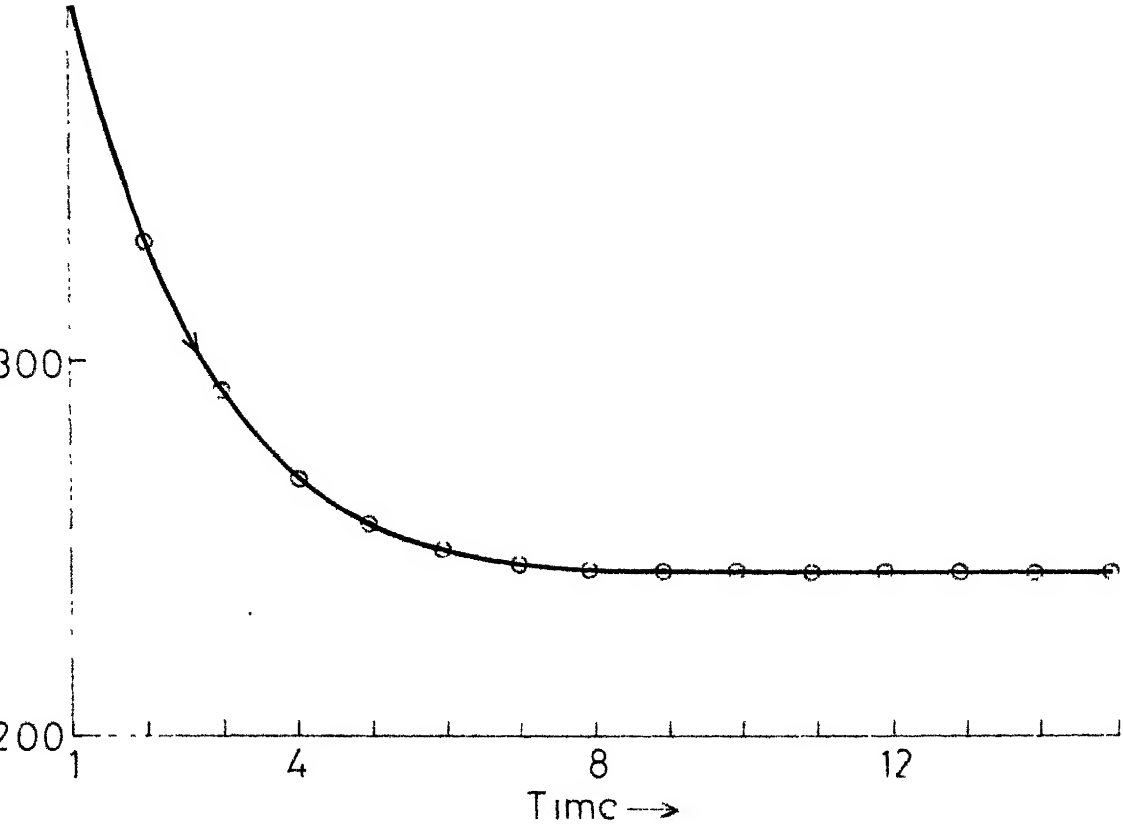
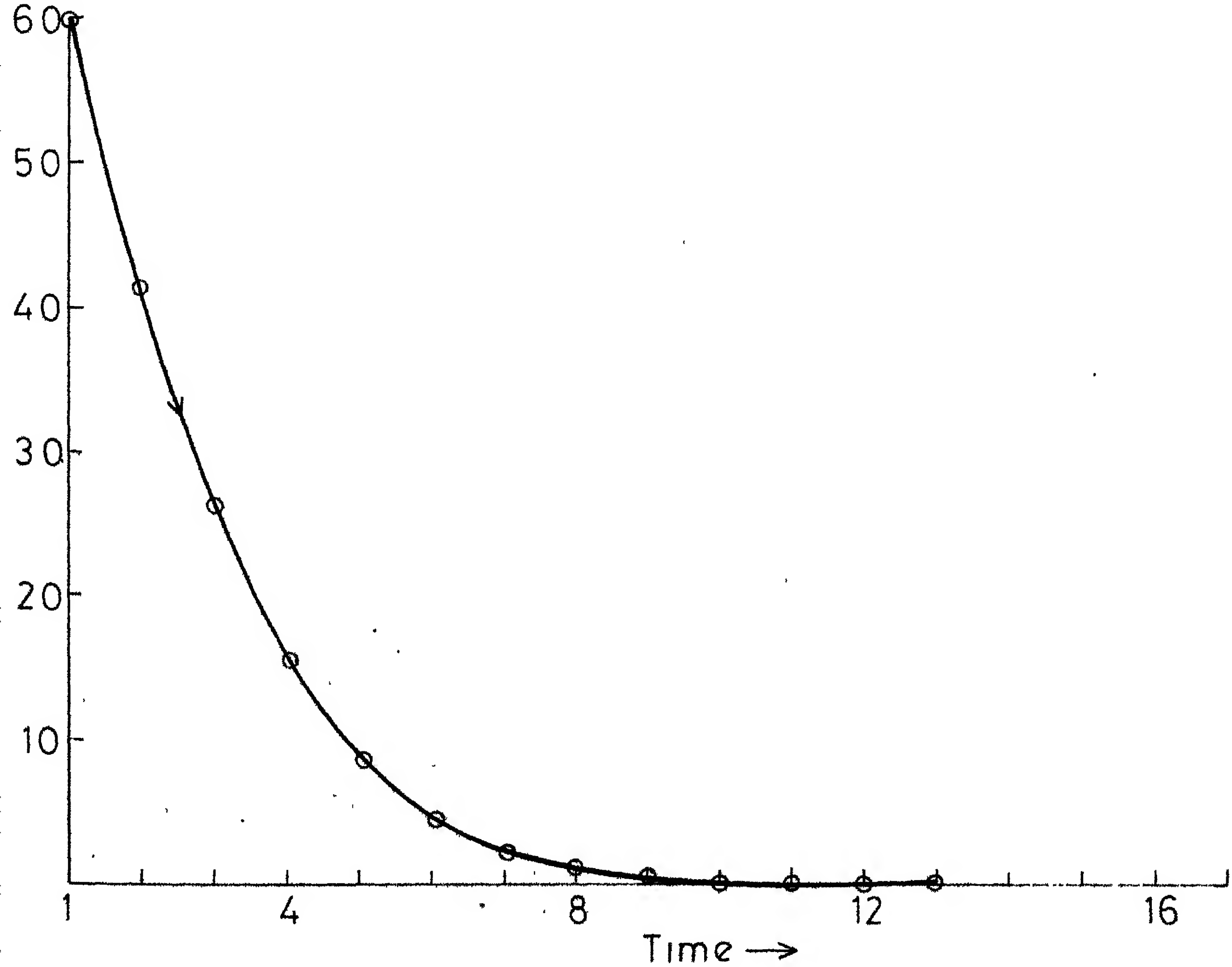


Fig 3.17



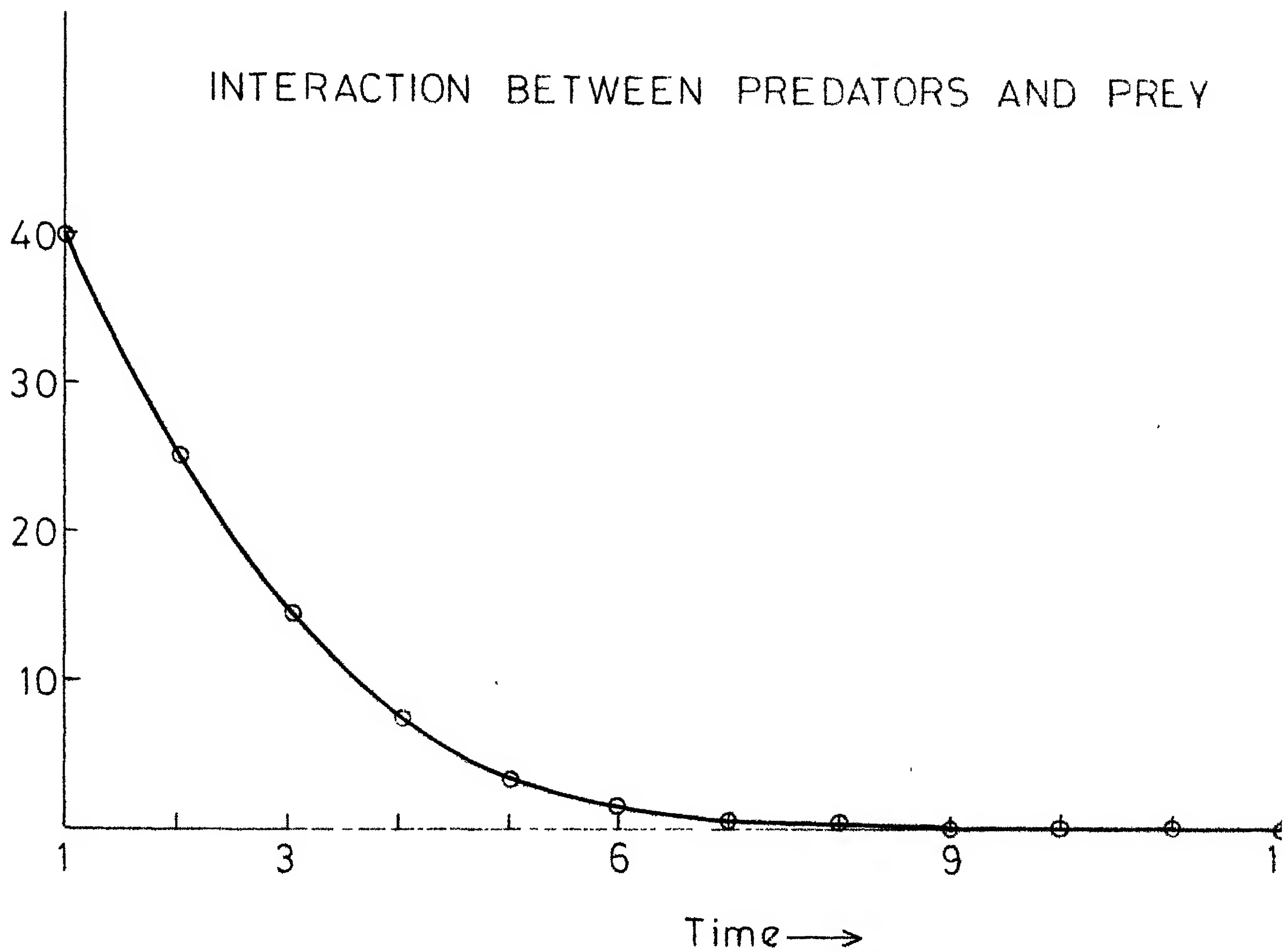

INTERACTION BETWEEN PREDATORS AND PREY
40
30
20
10
1
3
6
9
1
Time ⟶

Fig 3.19

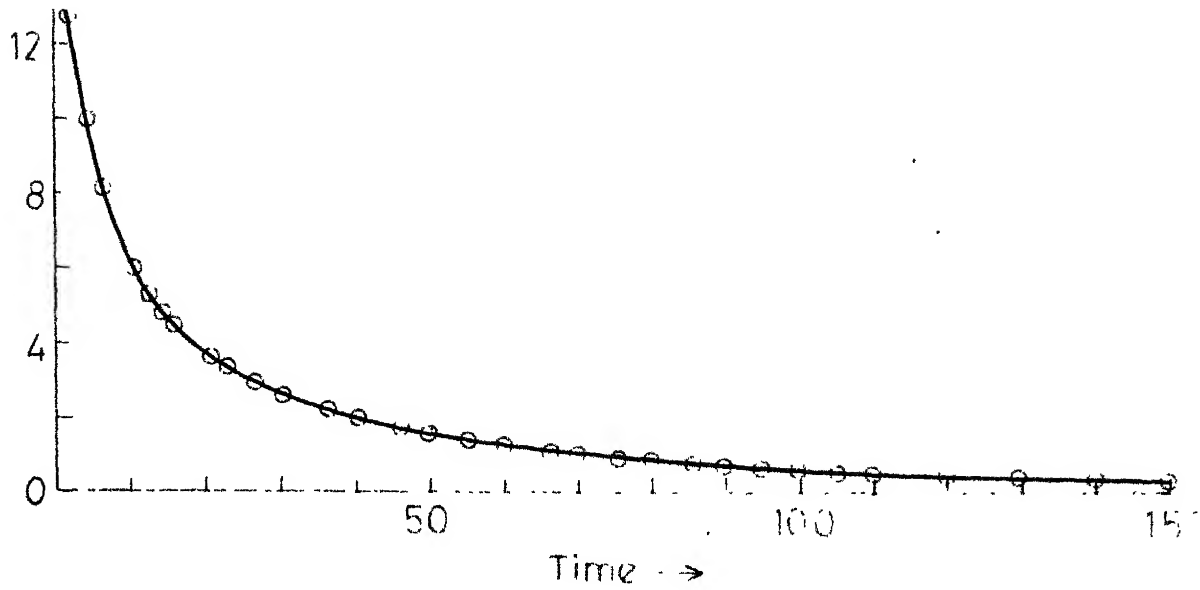


Fig 3.20

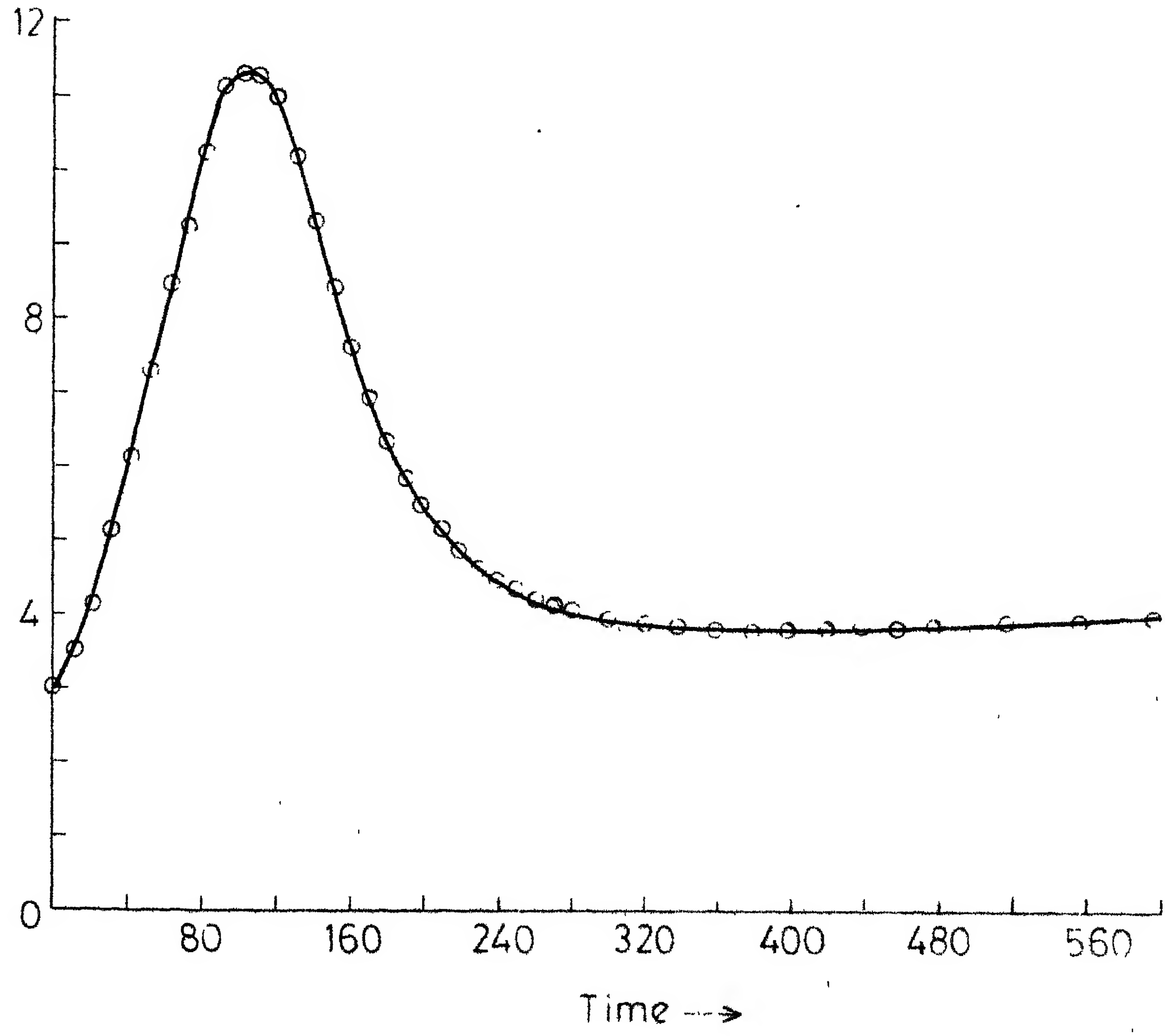


Fig 3.21

Prey population decreases exponentially and finally becomes extinct. Predator first increases upto certain value, after that it will decrease sharply and then again start increasing slowly.

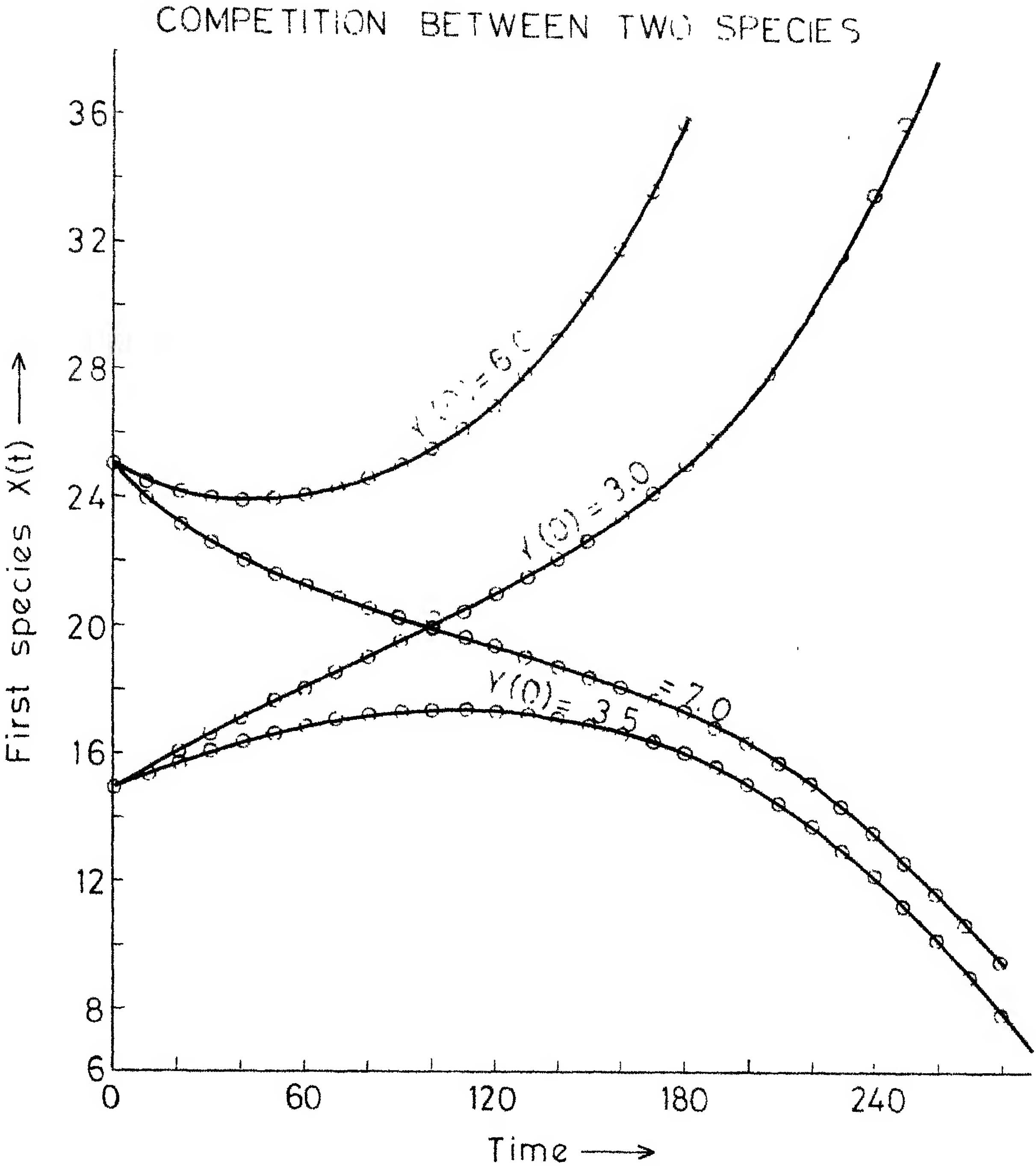
3.11 COMPETITION BETWEEN TWO SPECIES

In this, each species increases in the absence of the other by an amount proportional to its own population, but in the presence of the other, it decreases by an amount proportional to the product of the two so that our model is

$$\begin{aligned} X(t+1) - X(t) &= a_1 X(t) - b_1 X(t)\, Y(t) \\ Y(t+1) - Y(t) &= a_2 Y(t) - b_2 X(t)\, Y(t) \end{aligned} \tag{36}$$

Figures 3.22, 3.23, 3.24 give the graphs for the case when $a_1 = .01$, $a_2 = .02$, $b_1 = .002$, $b_2 = .001$ so that the equilibrium point is $X_e = 20$, $Y_e = 5$.

The survival of a species depends critically on initial size of the two populations. When $X(0) = 25$, $Y(0) = 7$ or $X(0) = 15$, $Y(0) = 3.5$, the first species tends to disappear and when $X(0) = 25$, $Y(0) = 6$ or $X(0) = 15$, $Y(0) = 3$, the second species tend to disappear. When $X(0) = 25$, a change of $Y(0)$ from 6 to 7 makes the second species survive and the first species to disappear. A similar effect is seen when $X(0) = 15$ and $Y(0)$ changes from 3 to 3.5.



COMPETITION BETWEEN TWO SPECIES
First species X(t) →
Time →
36
32
28
24
20
16
12
8
6
0
60
120
180
240
Y(0)=6.0
Y(0)=3.0
Y(0)=3.5
=7.0

Fig 3 22

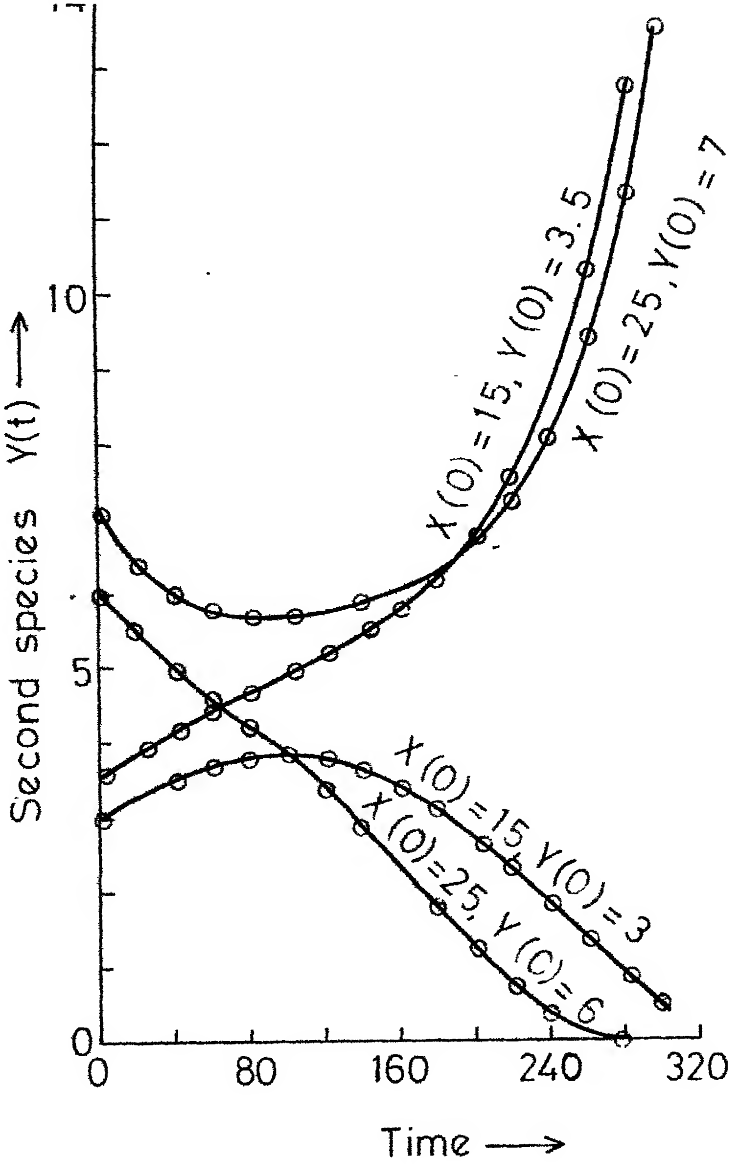


Fig. 3.23

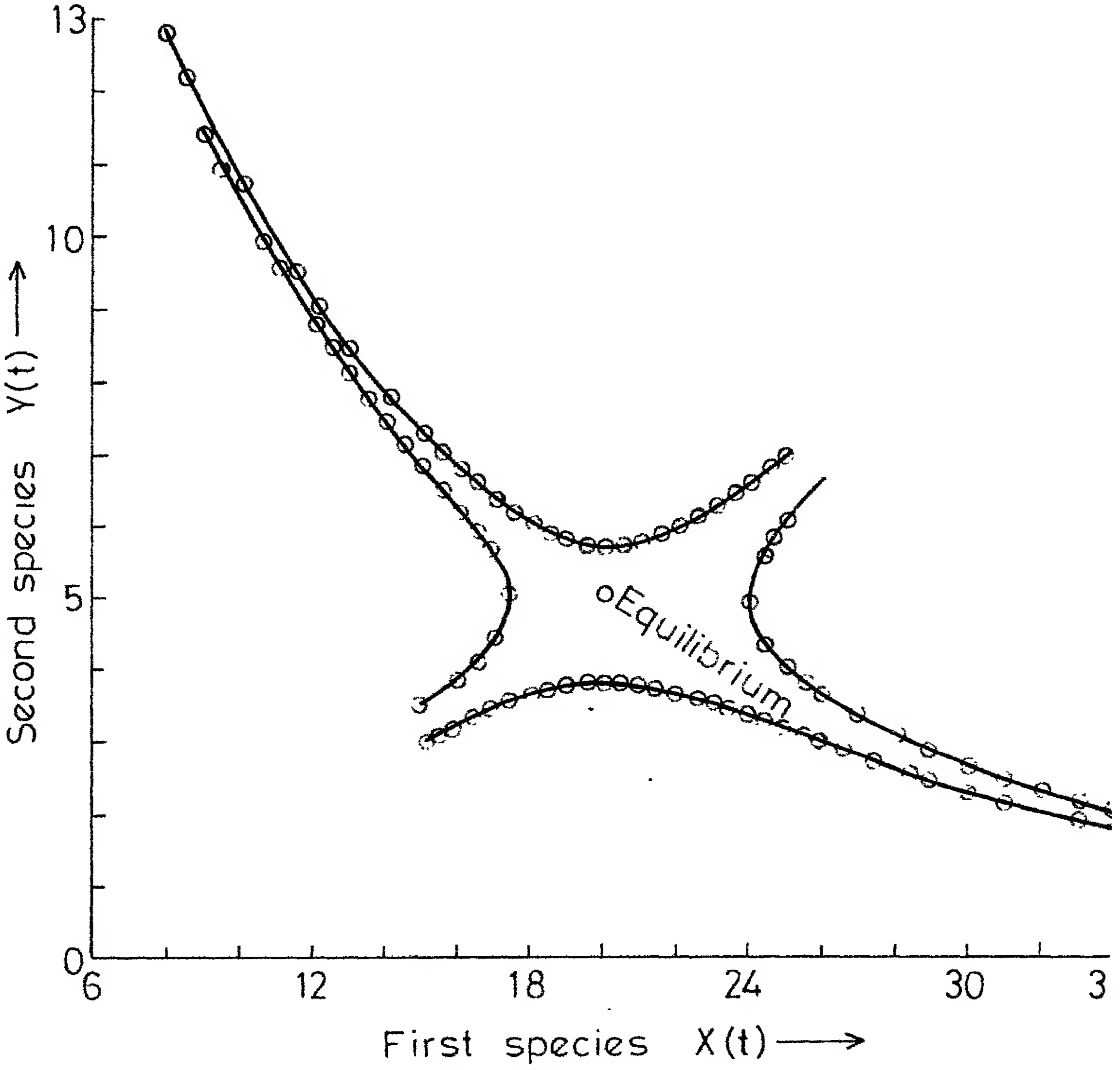


Fig 3.24

If out of the two species, only one is of the desirable type, we can ensure its survival and the vanishing of the other by just adjusting the initial populations.

If self interaction is also taken into account then the above model represented by the equation (36) will become

$$\begin{aligned} X(t+1)-X(t) &= a_1X(t) - b_1X^2(t) - c_1X(t)\,Y(t) \\ Y(t+1)-Y(t) &= a_2Y(t) - b_2Y^2(t) - c_2X(t)\,Y(t) \end{aligned} \tag{37}$$

both species will decrease by an amount proportional to the product of its own population.

Population growth of first competing species is shown in figure 3.25 and of second in Figure 3.26 while the combined behaviour of both species with respect to time is shown in Figure 3.27.

In sub figure 1

$a_1 = .01$ $a_2 = .02$ $X(0) = 15.0$

$b_1 = .02$ $b_2 = .03$ $Y(0) = 3.0$

$c_1 = .002$ $c_2 = .001$

In this case second species will grow while first species will die out.

In sub figure 2,

$a_1 = .01$ $a_2 = .02$ $X(0) = 21.0$

$b_1 = .005$ $b_2 = .008$ $Y(0) = 6.0$

$c_1 = .002$ $c_2 = .001$

In this case both species will die out.

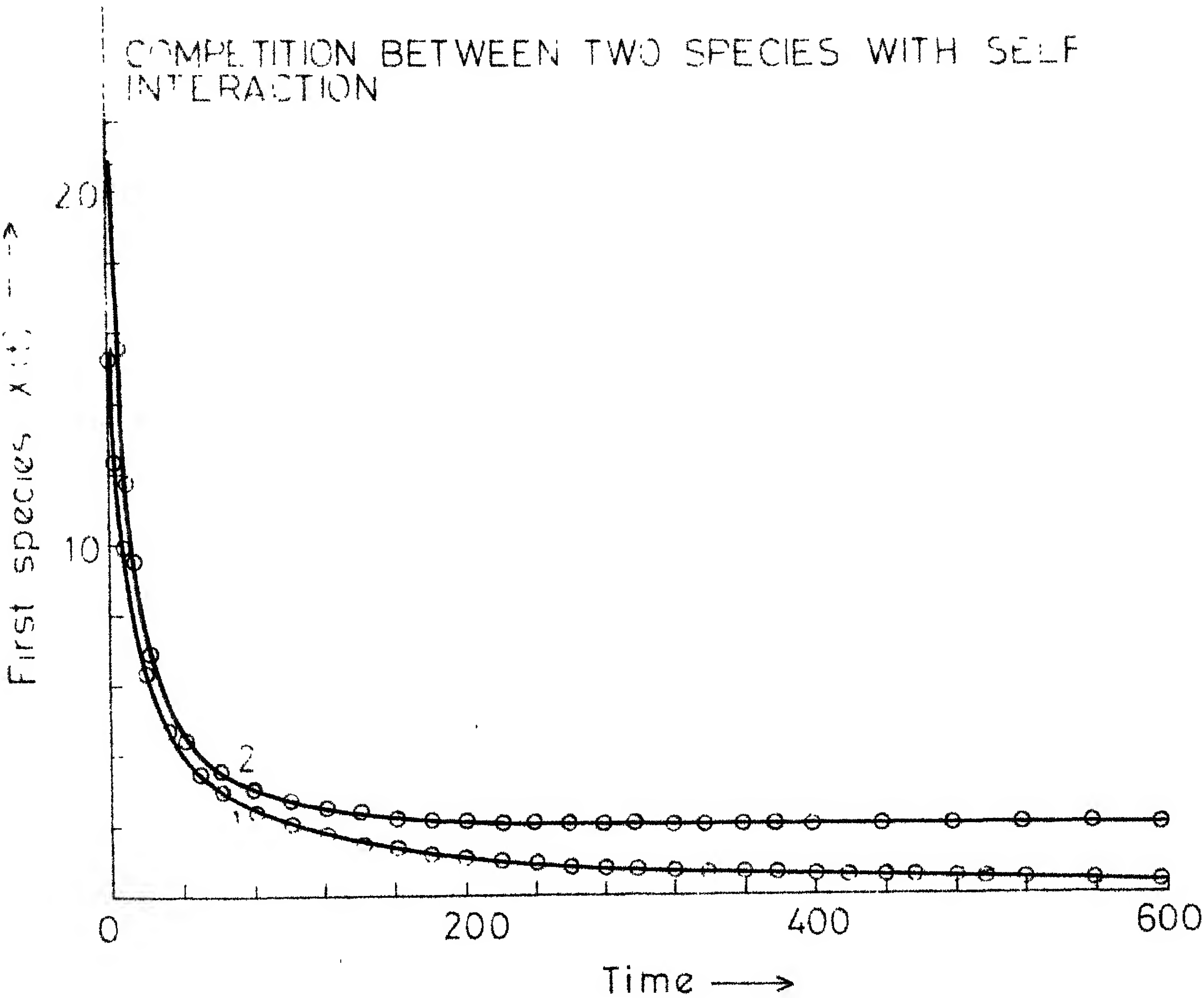

COMPETITION BETWEEN TWO SPECIES WITH SELF INTERACTION
First species x(t)
Time
20
10
0
200
400
600
2
1

Fig. 3.25

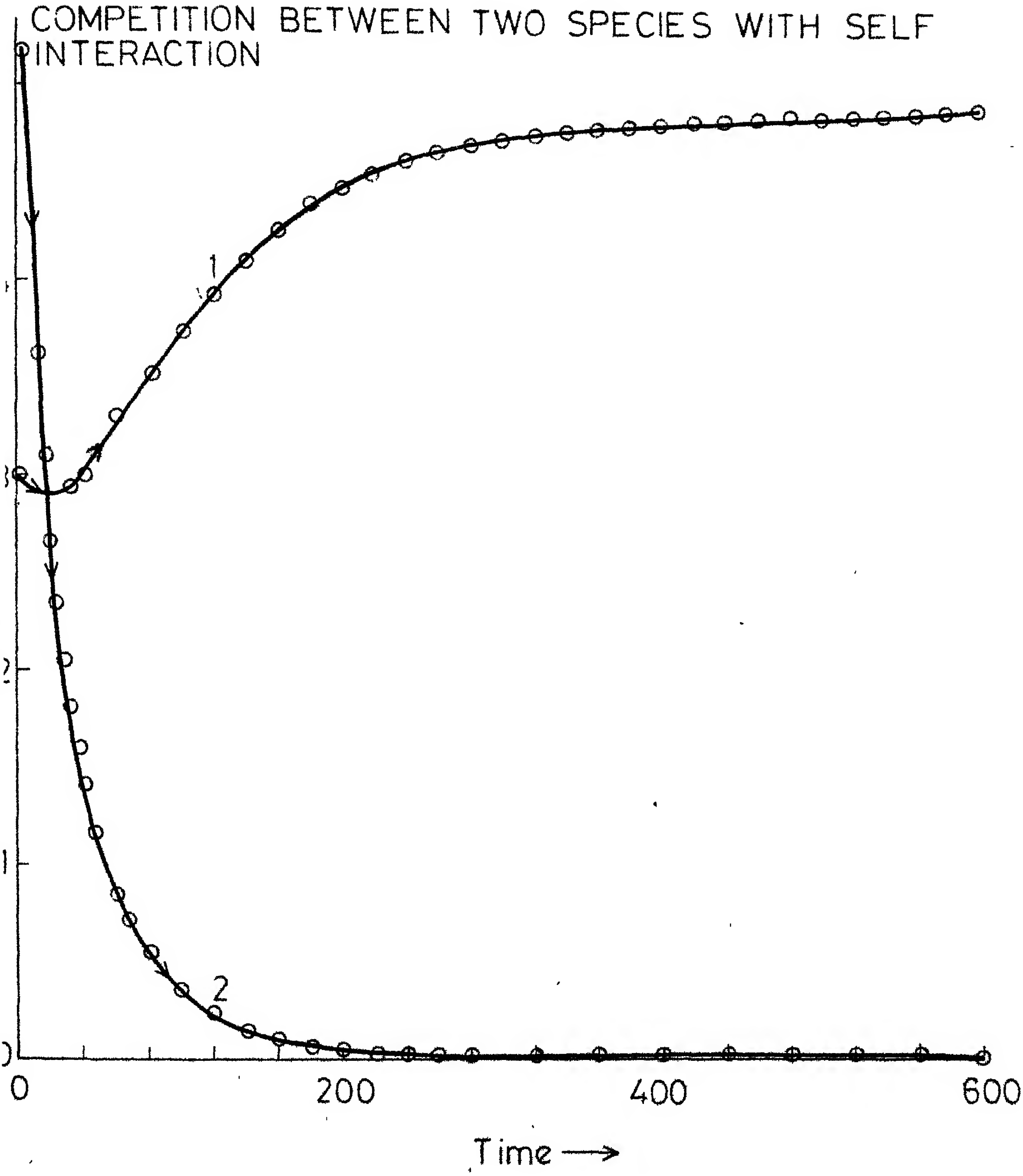

COMPETITION BETWEEN TWO SPECIES WITH SELF INTERACTION
1
2
0
200
400
600
Time ⟶

Fig. 3.26

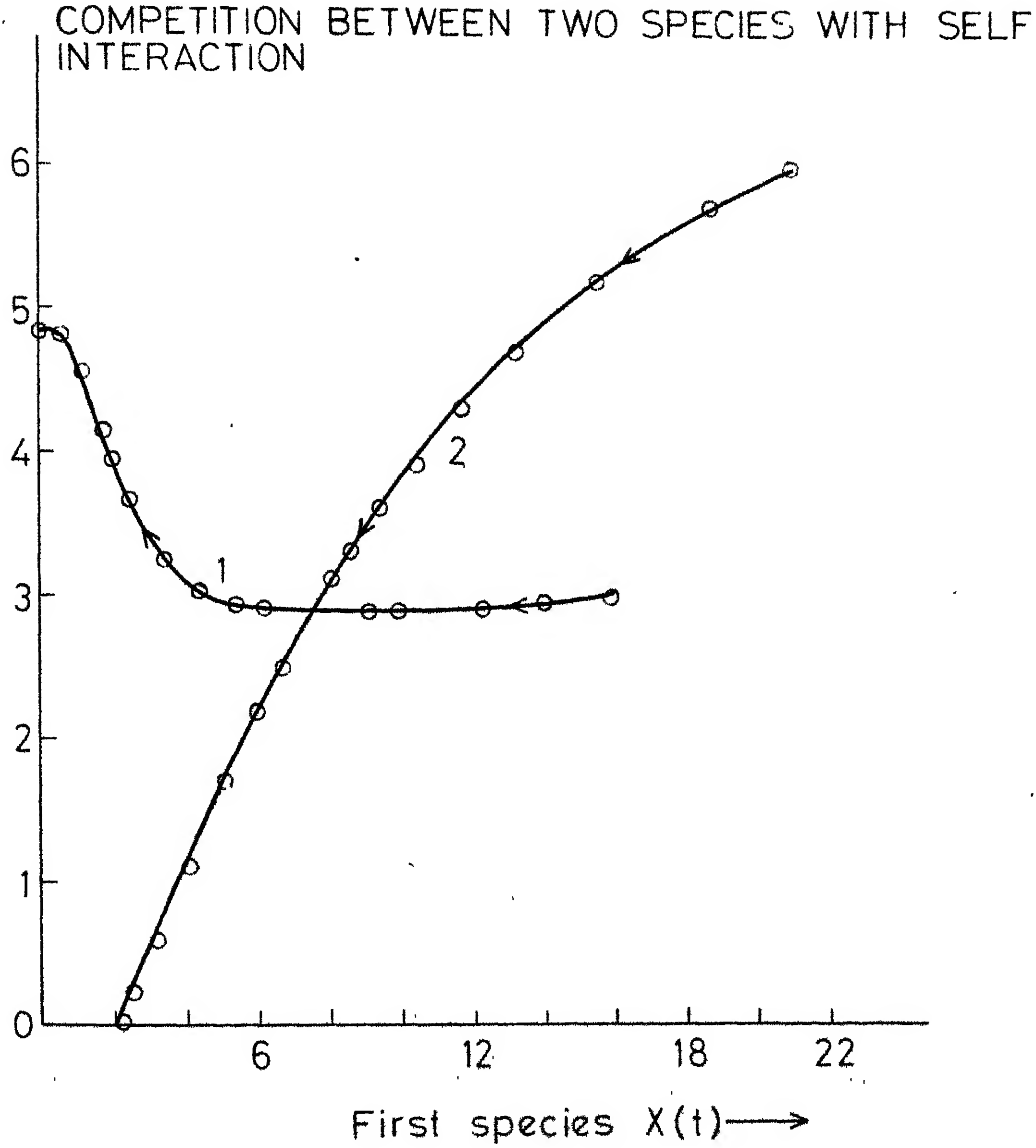

COMPETITION BETWEEN TWO SPECIES WITH SELF INTERACTION
6
5
4
3
2
1
0
1
2
6
12
18
22
First species X(t)

Fig 3.27

3.12 COMPETITION AMONG THREE SPECIES

In this model, each species grows in the absence of others, but mutual contacts are harmful since they are competing for the same resources. Our model can also represent three tribes at war with each other.. The model is

$$\begin{aligned} X(t+1)-X(t) &= a_1X(t)-a_2X(t)Y(t) - a_3X(t)Z(t) \\ Y(t+1)-Y(t) &= b_1Y(t)-b_2Y(t)X(t) - b_3Y(t)Z(t) \\ Z(t+1)-Z(t) &= c_1Z(t)-c_2Z(t)X(t) - c_3Z(t)Y(t) \end{aligned} \qquad (38)$$

The graphs below corresponding to the following values

$a_1 = .01$, $a_2 = .001$, $a_3 = .002$, $b_1 = .002$, $b_2 = .002$

$b_3 = .003$, $c_1 = 0.03$, $c_2 = 0.03$, $c_3 = 0.004$

are shown in figures 3.28-3.32

The equilibrium point is

$$X_e = 0.6, \quad Y_e = 3.4, \quad Z_e = 3.6$$

sub figure. correspondsto $X(0) = 5.0$, $Y(0)=7.0$, $Z(0)=7.0$

sub figure. correspondsto $X(0) = 7.0$, $Y(0)=10.0$, $Z(0)=10.0$

It appears that for case (i), the first two species disappear and the third species alone survives, while in case (ii) with different initial values, the first and third species tend to disappear and the second species alone survives. This again illustrates how initial population sizes can play a critical role in the survival of the species.

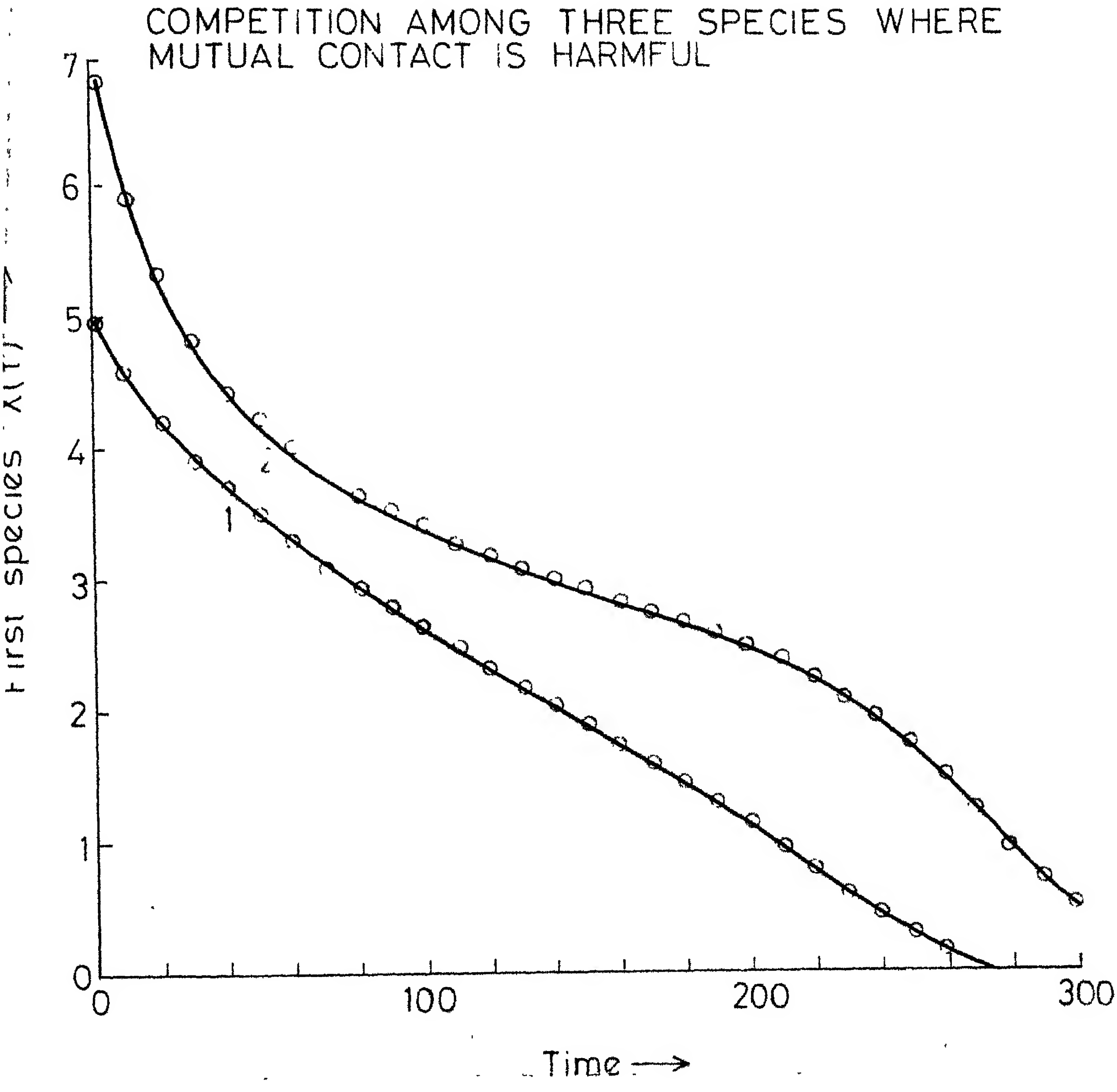

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL
First species X(T) →
Time →
0
100
200
300
1
2
3
4
5
6
7
1
2

Fig 3.28

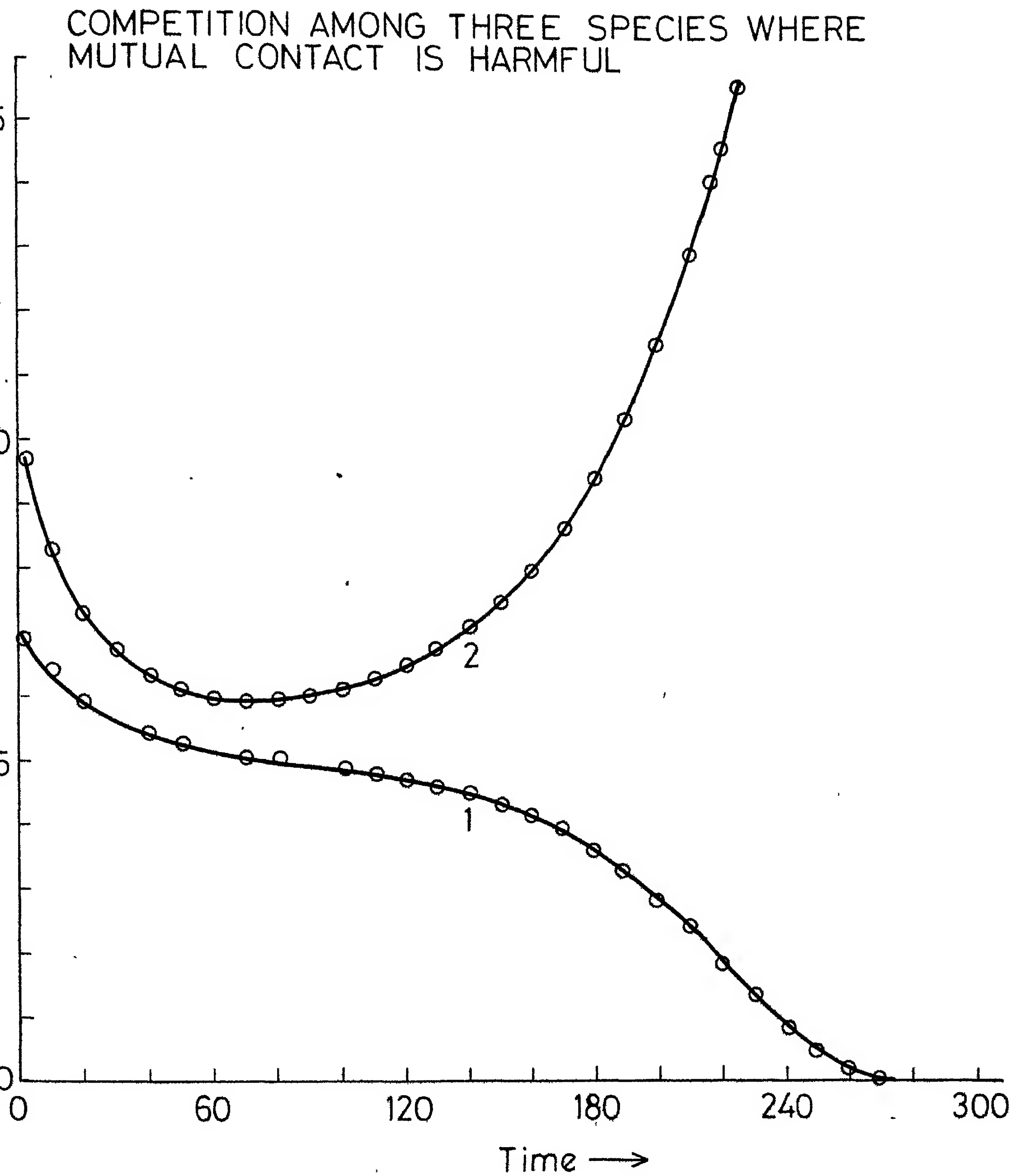

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL
2
1
0
60
120
180
240
300
Time →

Fig. 3.29

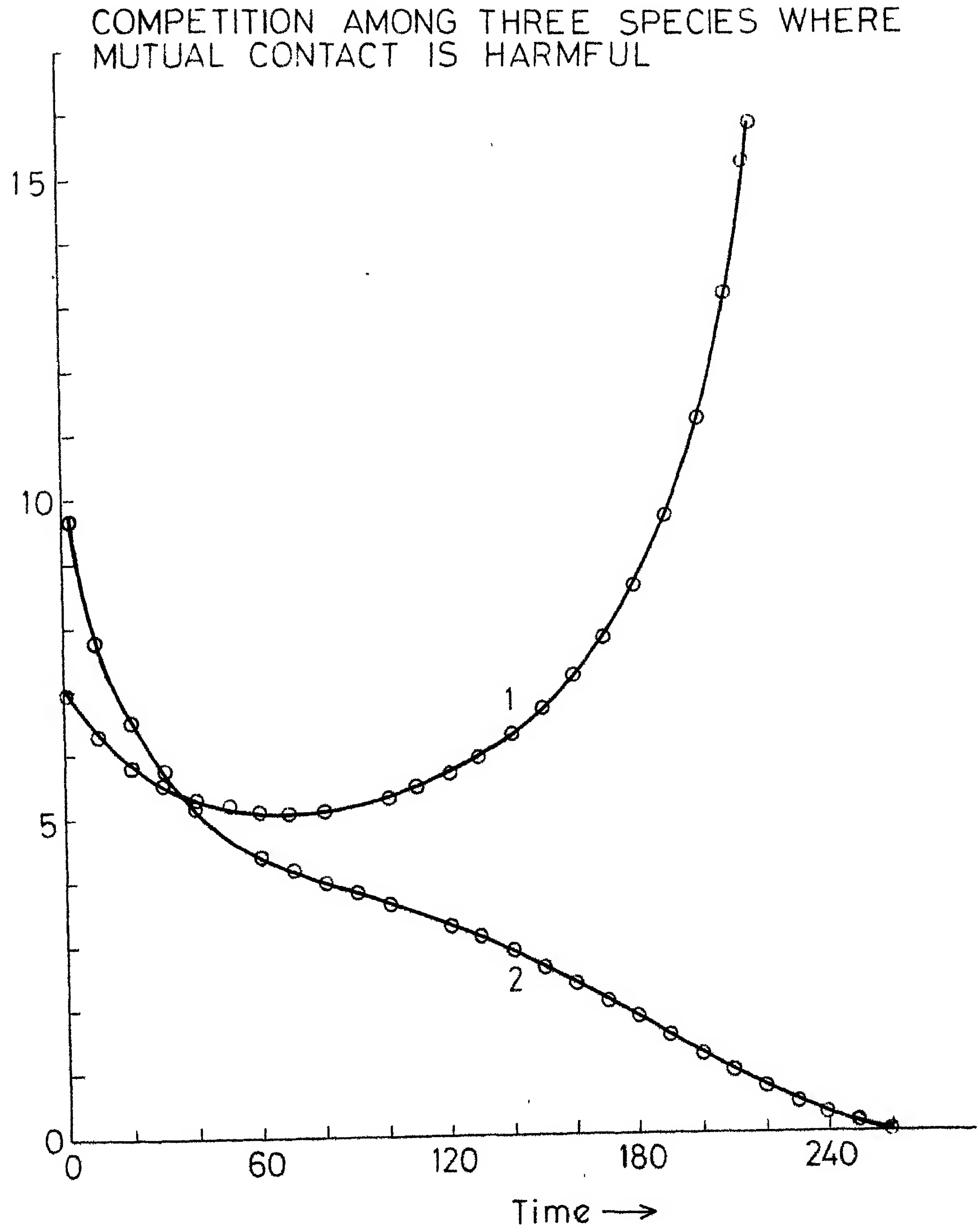

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL
15
10
5
0
1
2
0
60
120
180
240
Time ⟶

Fig. 3.30

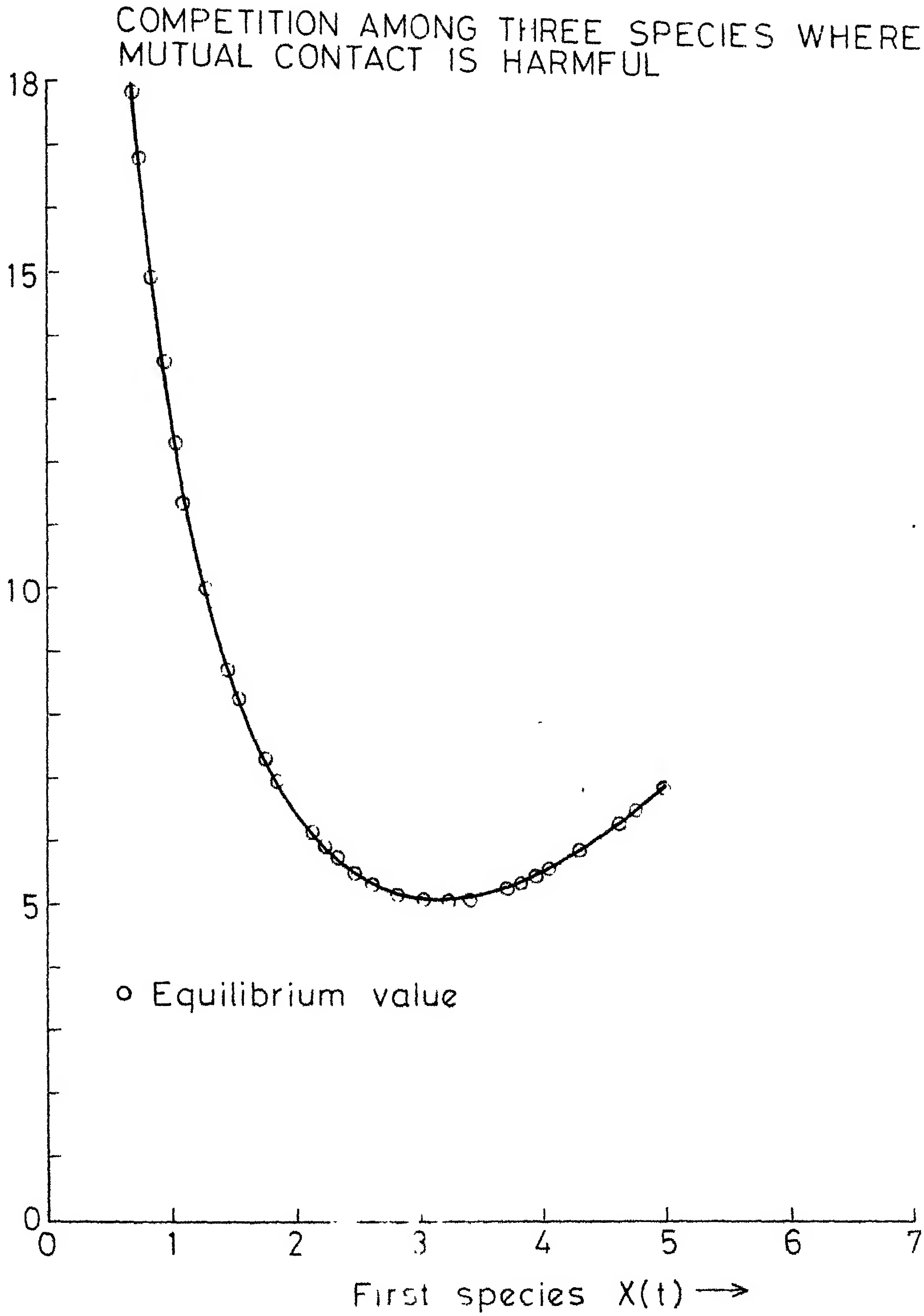

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL
18
15
10
5
0
0
1
2
3
4
5
6
7
o Equilibrium value
First species X(t) →

Fig 3.31

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL

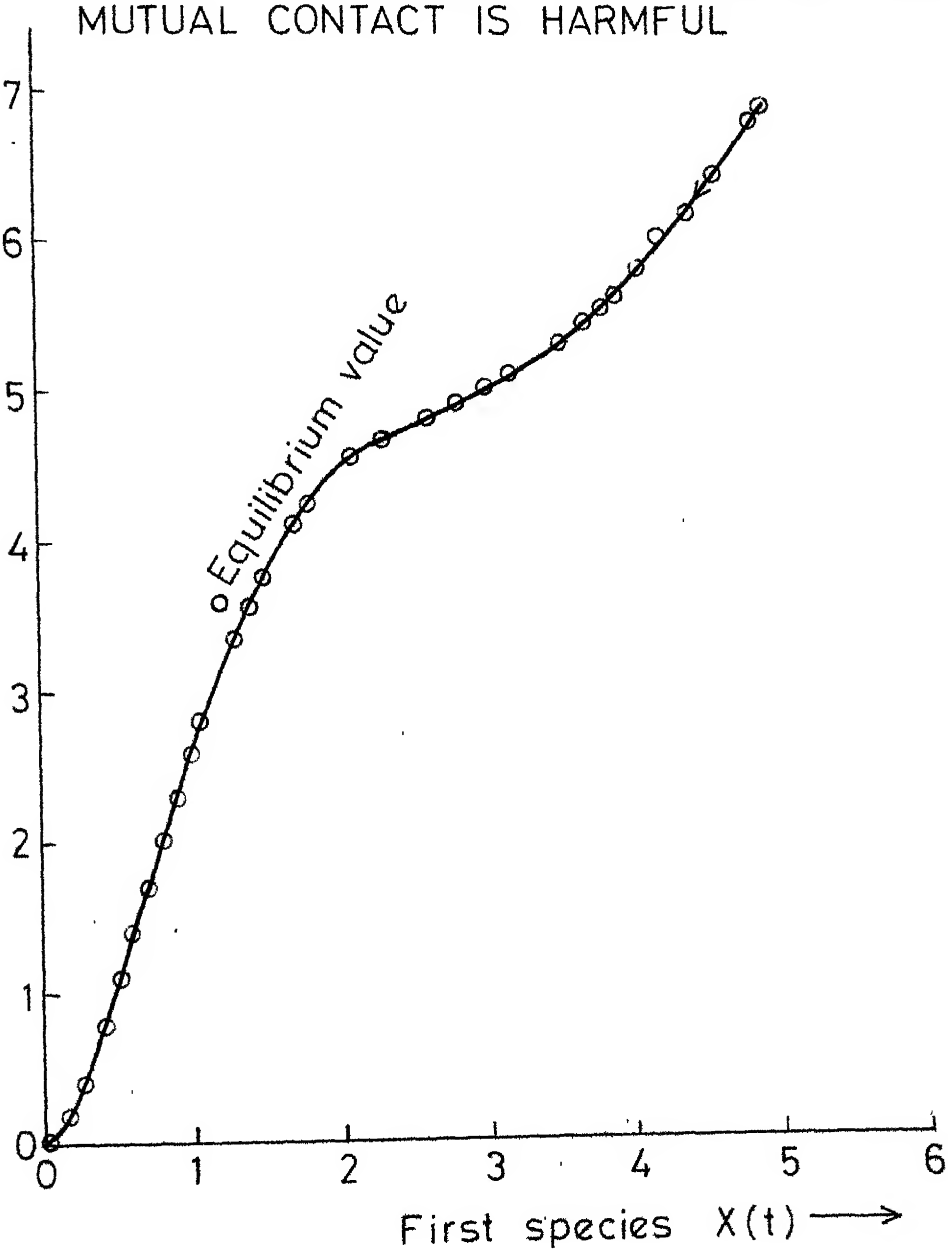


Fig. 3.32

In this model each species grows in the absence of other, but mutual contacts with remaining two are useful for first species. For second species, mutual contact with third is useful but harmful to first. Mutual contacts are harmful to the third species with remaining two. The model is

$$
\begin{aligned}
X(t+1)-X(t) &= AX(t)+BX(t)Y(t) + cX(t)Z(t) \\
Y(t+1)-Y(t) &= DY(t)+EY(t)Z(t) - FX(t)Y(t) \qquad (39) \\
Z(t+1)-Z(t) &= GZ(t)-HY(t)Z(t) - KX(t)Z(t)
\end{aligned}
$$

The graphs corresponding to the following values

$A = .01 \quad B = .001 \quad C = .002 \quad D = .04 \quad E = .002$

$F = .003 \quad G = .03 \quad H = .003 \quad K = .008$

are shown in Figures 3.33–3.38

Sub Figure 1 corresponds to $X(0)=35.0$, $Y(0) = 20.0$ $Z(0) = 35.0$

Sub Figure 2 corresponds to $X(0)=25.0$, $Y(0) = 9.0$, $Z(0) = 25.0$

It appears for both cases, the first species only survives while second and third will disappear.

3.13 EPIDEMIC MODEL WITHOUT REMOVAL

Let $X(t)$ denote the number of susceptible and $Y(t)$ infectives at time t. In the time interval $(t,t+1)$, $X(t)$ decreases by $\beta X(t)\,Y(t)$ and $Y(t)$ increases by the same amount so that

$$
\begin{aligned}
X(t+1)-X(t) &= -\beta X(t)Y(t) \qquad (40) \\
Y(t+1)-Y(t) &= \beta X(t)Y(t)
\end{aligned}
$$

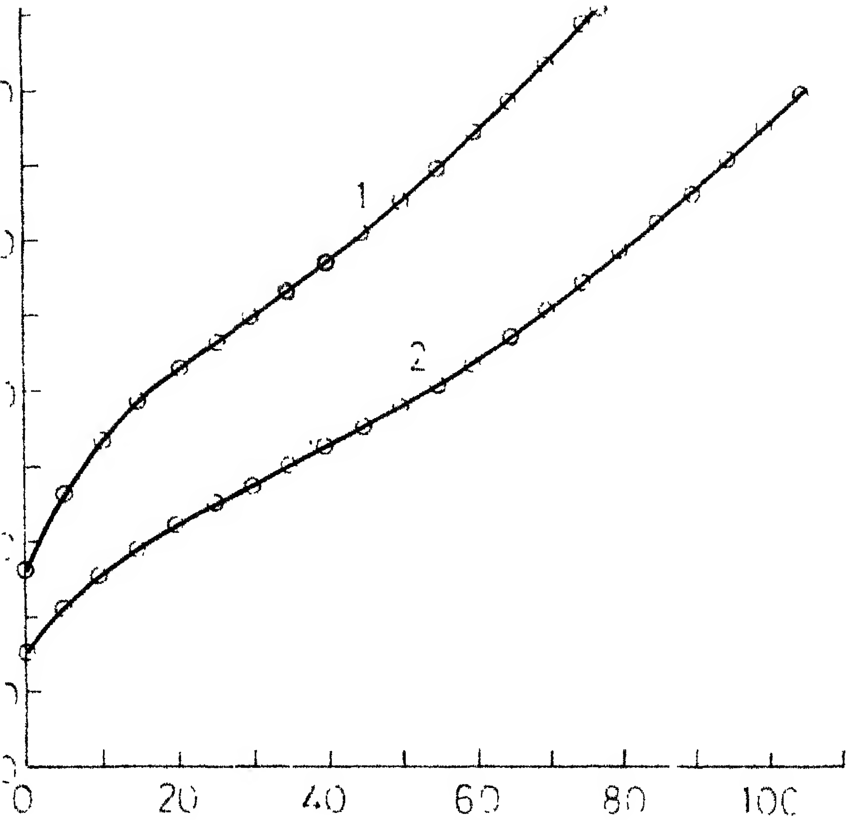
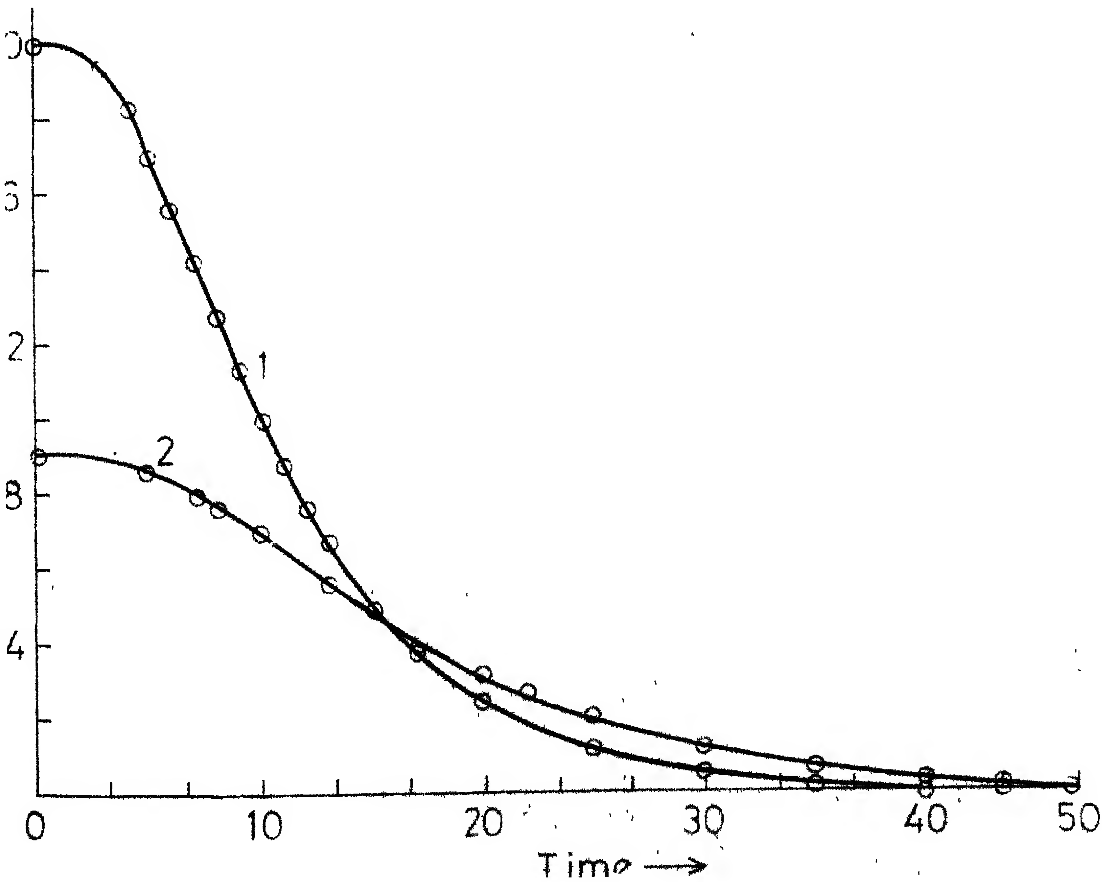


Fig 3.33



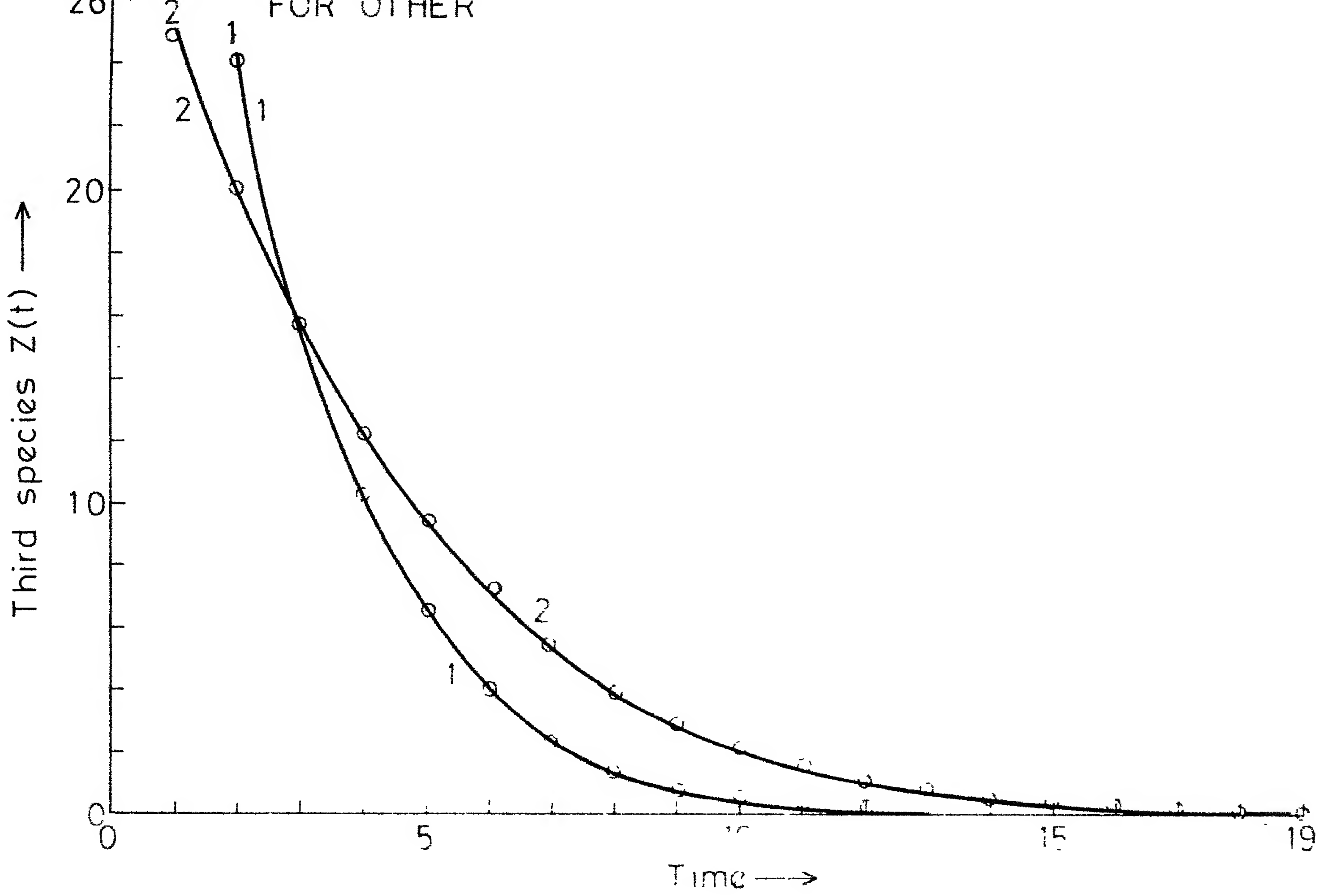


Fig 3 35

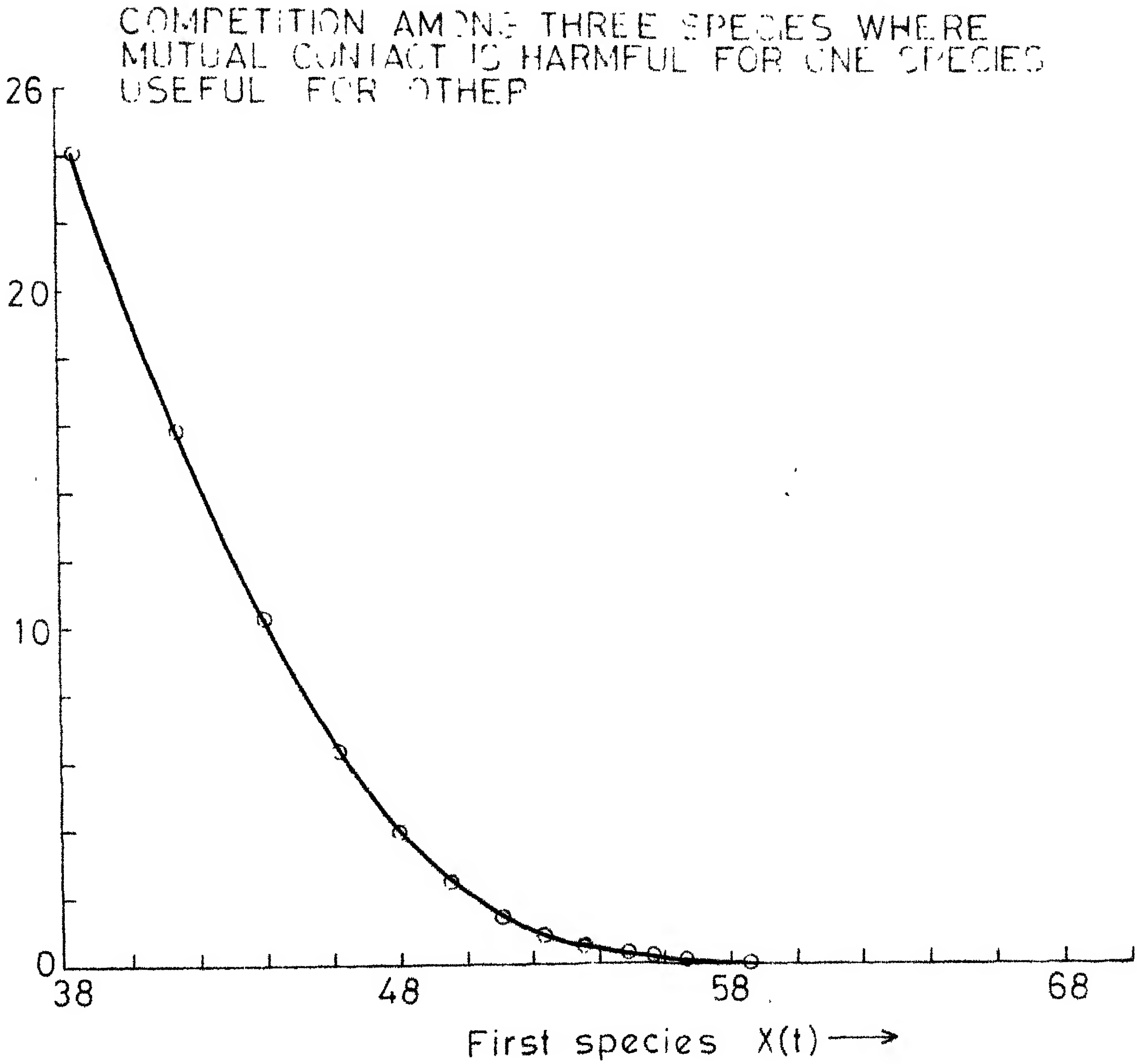

COMPETITION AMONG THREE SPECIES WHERE
MUTUAL CONTACT IS HARMFUL FOR ONE SPECIES
USEFUL FOR OTHER
26
20
10
0
38
48
58
68
First species X(t) ⟶

Fig. 3.36

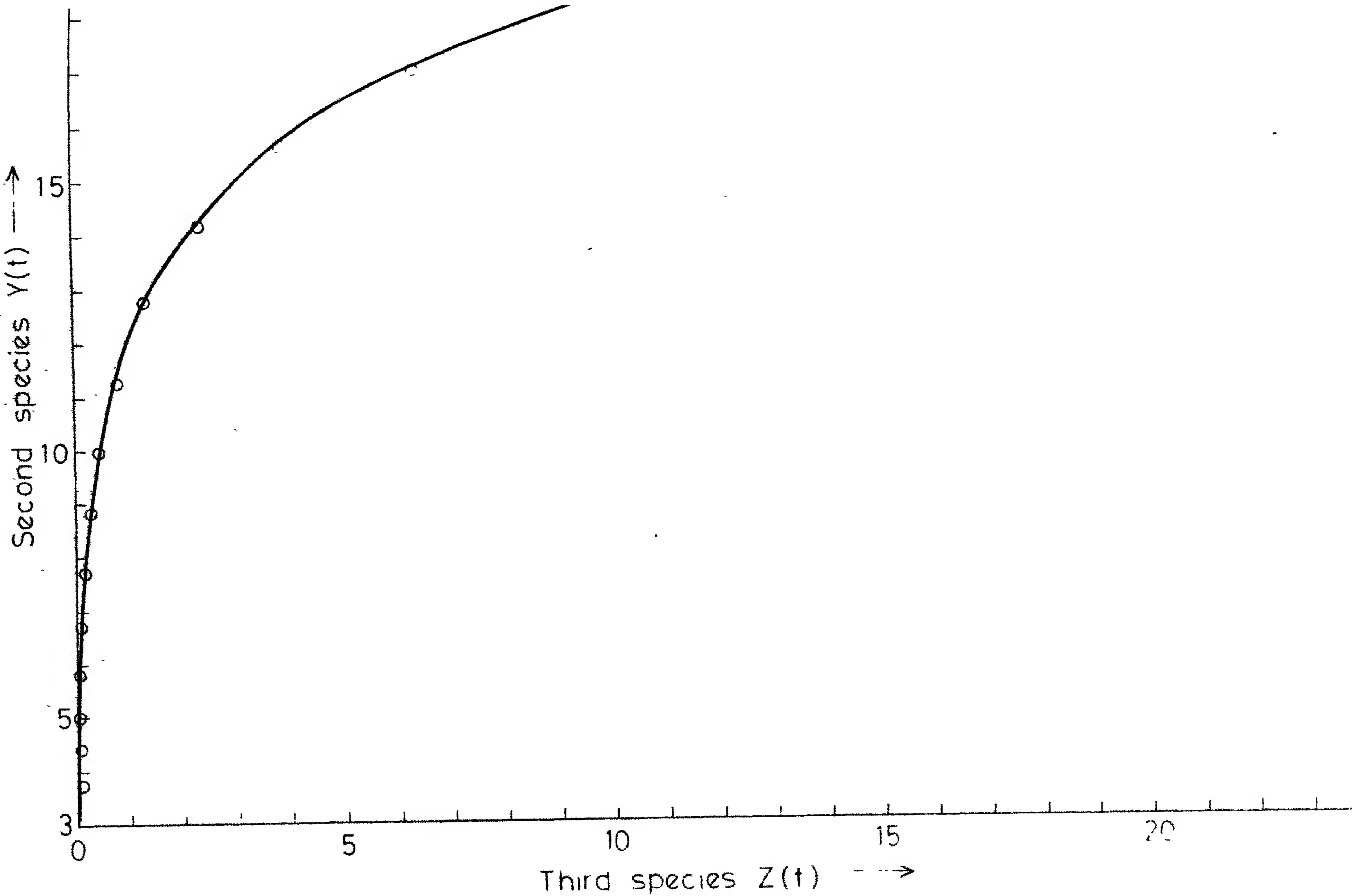


Fig. 3.37

COMPETITION AMONG THREE SPECIES WHERE MUTUAL CONTACT IS HARMFUL FOR ONE SPECIES AND USEFUL FOR OTHER

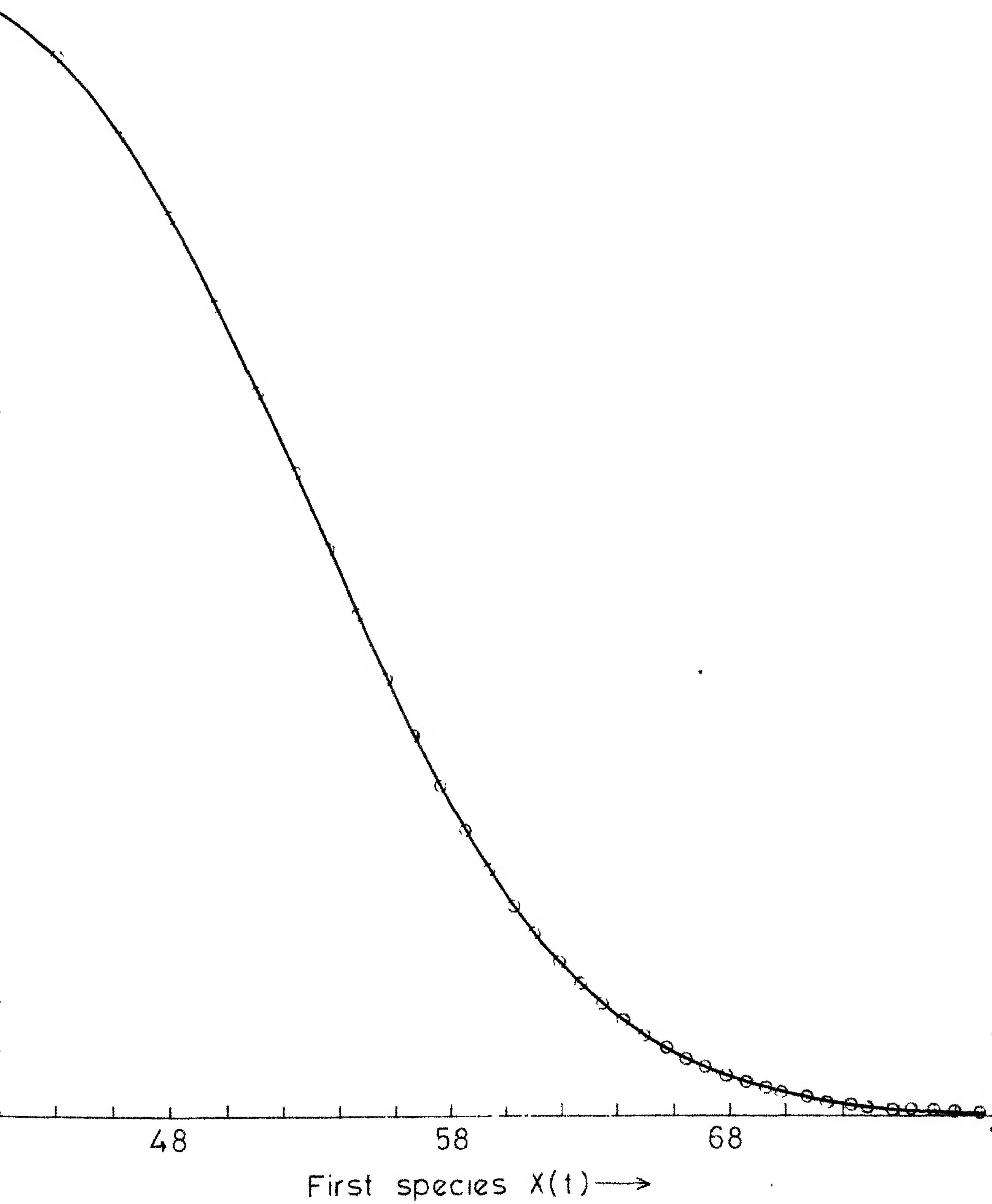


Fig. 3.38

Initially let there be n susceptibles and 1 infective, so that

$$X(0) = n, \; Y(0) = 1$$

From (40)

$$X(t+1)+Y(t+1) = X(t)+Y(t) = X(t-1)+Y(t-1) = \ldots X(0)+Y(0) = n+1 \tag{41}$$

so that the trajectories in the X-Y plane are straight lines.

From (40) and (41)

$$X(t+1) = X(t)-\beta X(t)[n+1-X(t)] = X(t)\,[1-\beta n-\beta] + \beta X^2(t), \tag{42}$$ *

so that

$$X(1) = n-n\beta, \; X(2) = n(1-\beta)\,(1-\beta-n\beta^2) \tag{43}$$

and we can successively find X(t) for any given value of t. The graphs of X(t) and Y(t) are given in Figures 3.39 and 3.40 for n = 10, β = .05, .03, .02, .01.

It appears that the number of suceptibles falls rapidly and the number of infectives rises rapidly and the greater the value of β, the greater is the rate of fall or rise.

3.14 EPIDEMIC MODEL WITH REMOVAL

In this case (40) becomes

$$\begin{aligned} X(t+1)-X(t) &= -\beta X(t)Y(t) \\ Y(t+1)-Y(t) &= \beta X(t)Y(t)-\gamma Y(t) \end{aligned} \tag{44}$$ **

so that

* See Note 6 of Appendix

** See Note 7 of Appendix

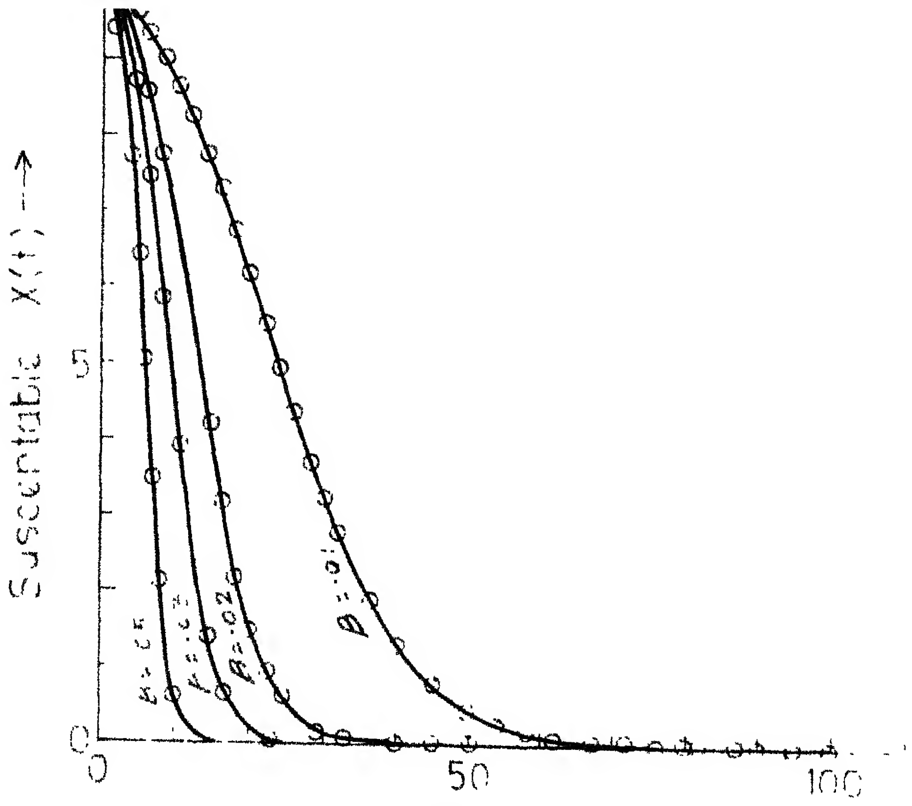


Fig 3 39

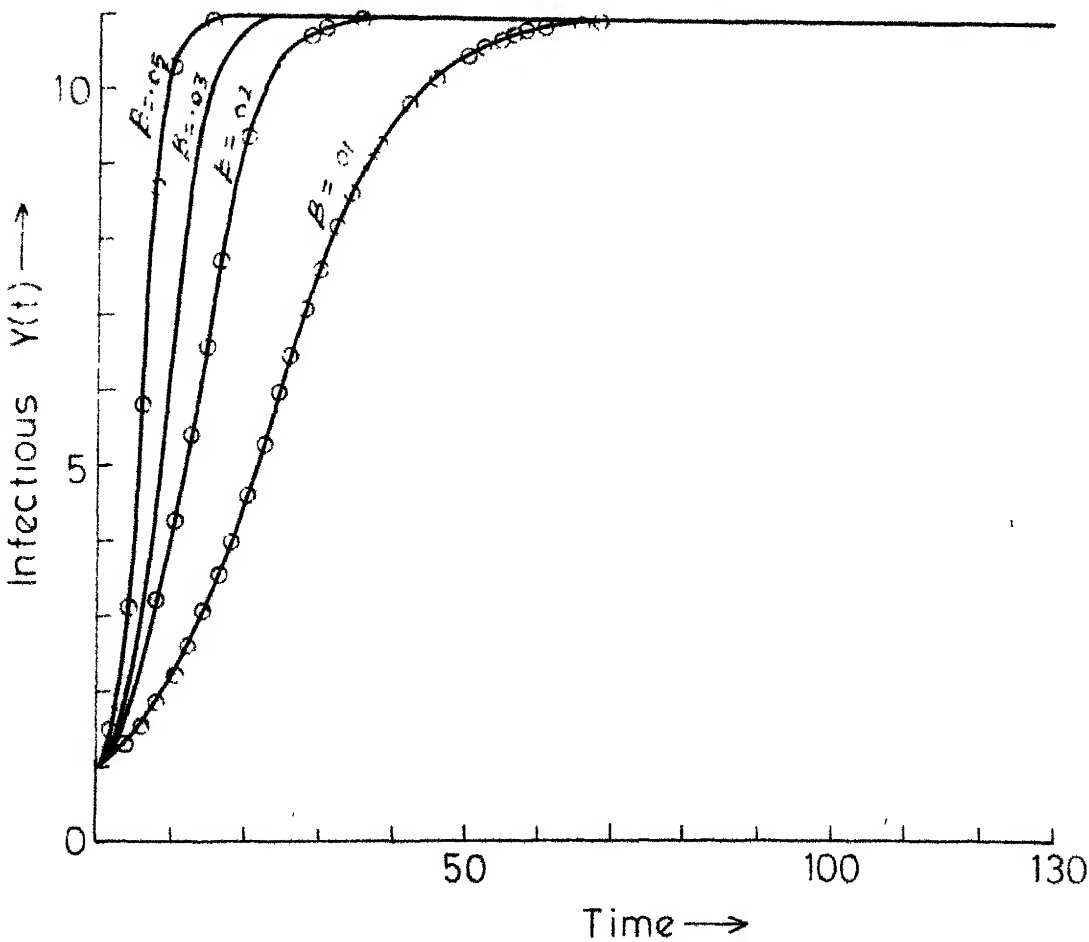


Fig.3.40

$$X(t+1)+Y(t+1) = X(t) + Y(t) - \gamma Y(t) \tag{45}$$

The graphs of X(t) and Y(t) are given below for

$n = 10$, $\beta = .01, .05, .1$, $\gamma = 0.1, 0.2$

Figure 3.41 Figure 3.42

It appears that the number of susceptible fall and the rate of fall increases with both β and γ. When β is large, it appears that the number of infective rises quickly and then falls.

3.15 GROWTH OF POPULATION WITH TIME-DELAY

Growth of a population with time-delay effect when abundant of food is available is studied. The model is

$$X(t+1)-X(t) = aX(t-30) \tag{46}$$

Behaviour of the population growth with respect to time is shown in fig. 3.43 for $a = .01$ and in Fig. 3.44 for $a = .04$.

For simplicity we consider that population remain constant i.e. $X(t) = 10$ upto $t = 30$. After $t = 30$ it will grow exponentially. The growth of the population is similar as in the model where time-delay is not considered.

3.16 GROWTH OF POPULATION WITH TIME-DELAY WITHOUT SUFFICIENT FOOD

Growth of a population when sufficient food is not available and the effect of past is considered, is studied. The model is

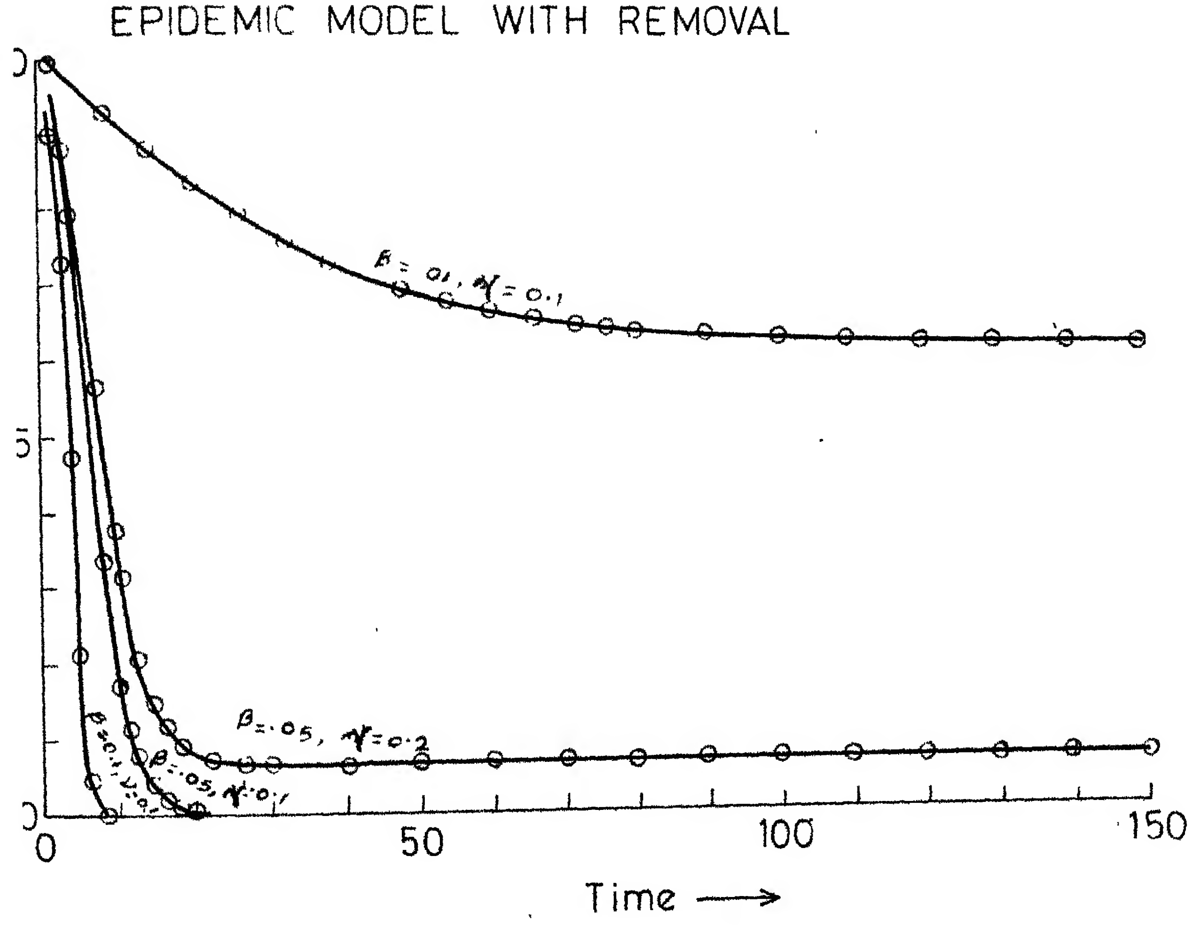

EPIDEMIC MODEL WITH REMOVAL
β = .01, γ = 0.1
β = .05, γ = 0.2
β = .05, γ = 0.1
0
50
100
150
Time →

Fig 3.41

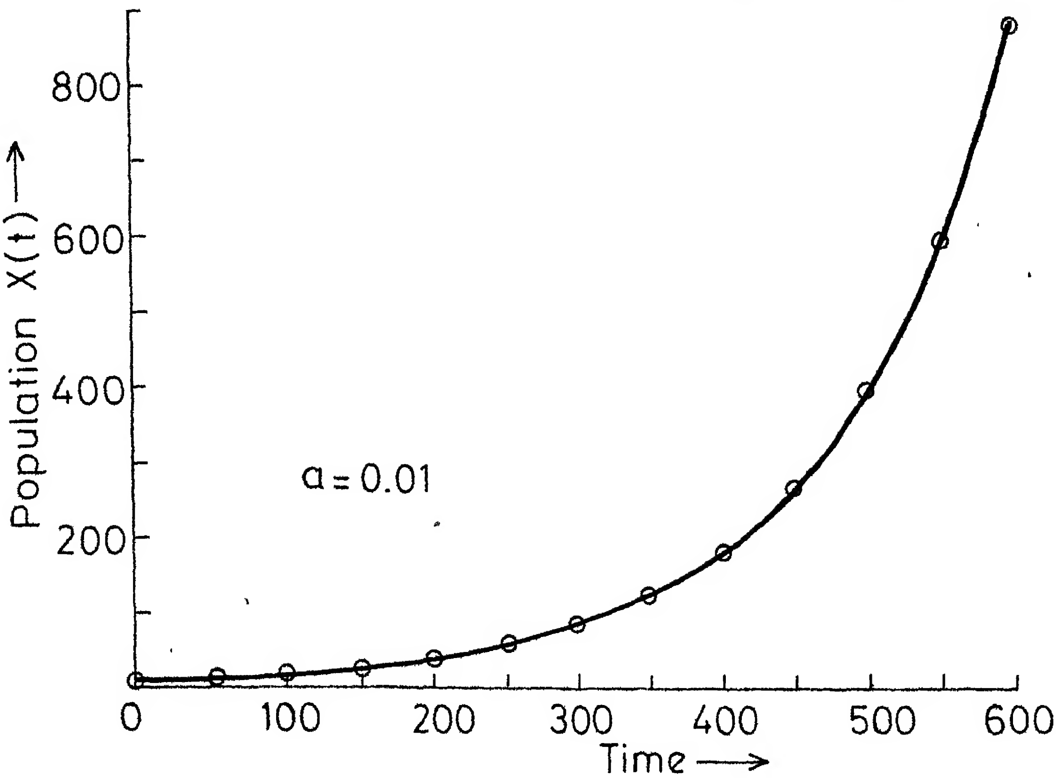
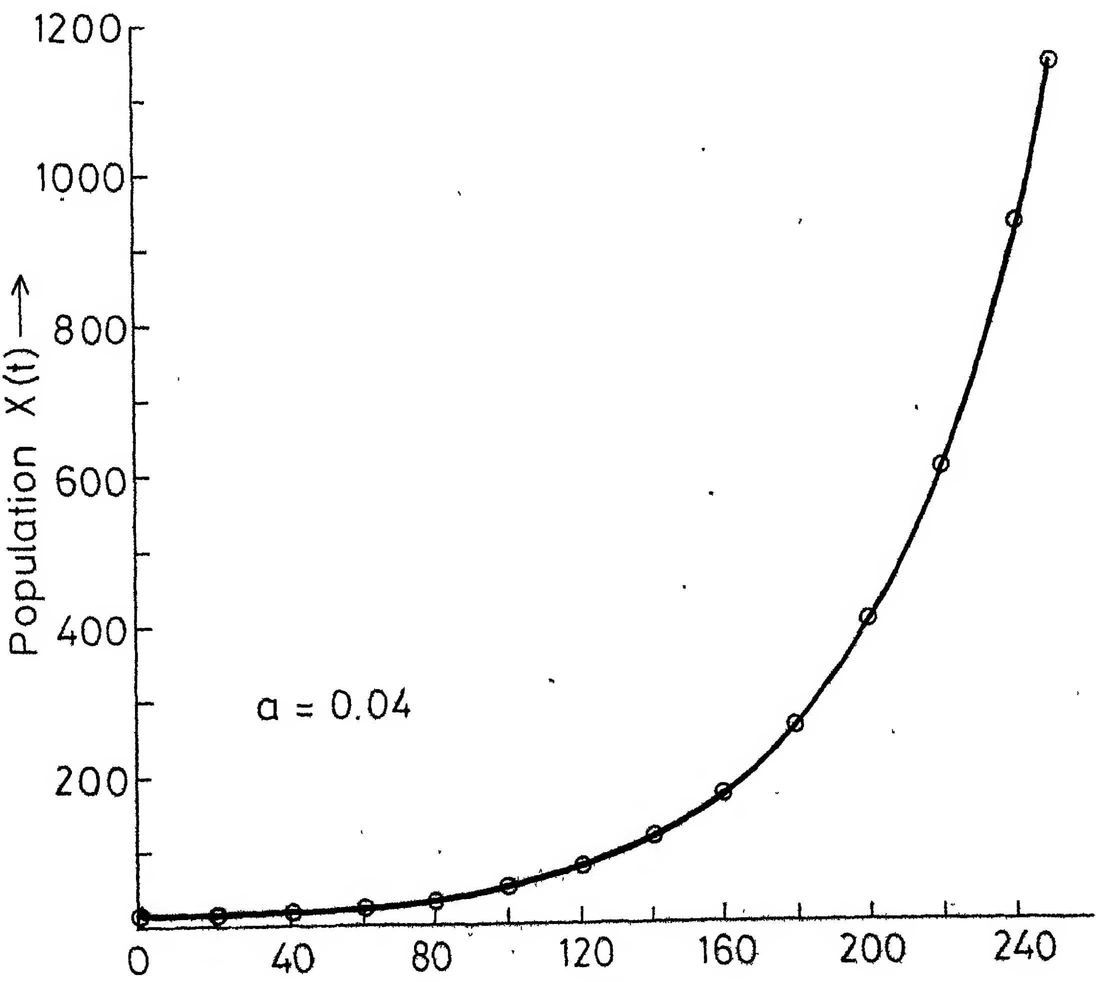

800
600
400
200
Population X(t)
a = 0.01
0
100
200
300
400
500
600
Time

Fig. 3.43


1200
1000
800
600
400
200
Population X(t)
a = 0.04
0
40
80
120
160
200
240

$$X(t+1)-X(t) = -aX(t) - bX(t-30) \qquad (47)$$

Due to shortage of food population will decrease. Behaviour of the population with respect to time is shown in Fig. 3.45 .

In sub Fig. 1 effect of shortage of food per unit population is the same as the time-delay effect on unit population i.e.

$$a = .001 \quad \text{and} \quad b = .001$$

In rest of sub figures effect of the shortage of food per unit population is more than the effect of past on unit population

i.e. in Sub Fig. 2 $a = .01$ and $b = .008$

Sub Fig. 3 $a = .01$ and $b = .005$

For simplicity we consider that population remains constant i.e. $X(t) = 10$ upto $t = 30$. After $t = 30$ it will decrease and vanish.

3.17 PREY-PREDATOR MODEL WITH TIME-DELAY*

It is possible that the reproductive rate depends, not only on the population density at the present time, but on the population density in the past. The reproductive rate of a predator species will depend on the prey, which may in turn depend on how much of the prey was eaten by predator in the last years. To gain some idea of the effect of such a delay in the effects of population density a model is given by

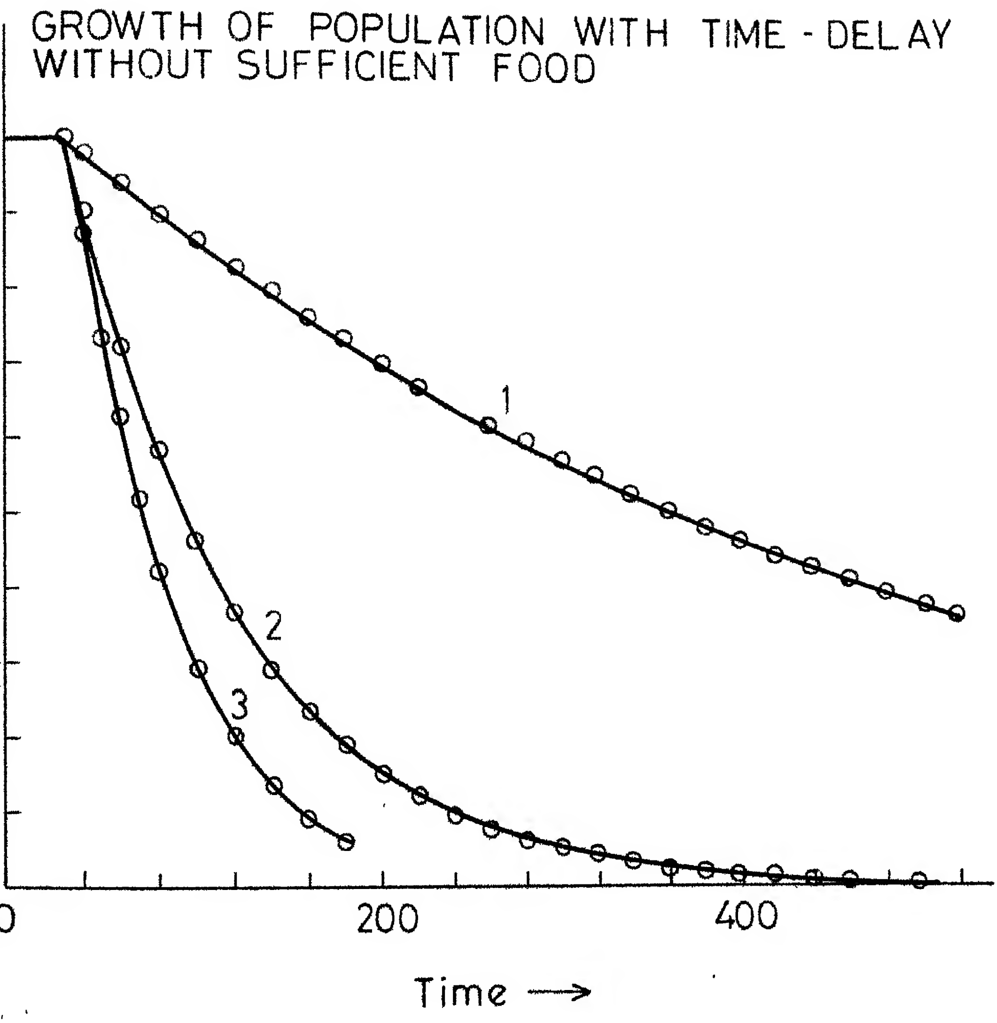

GROWTH OF POPULATION WITH TIME - DELAY WITHOUT SUFFICIENT FOOD
1
2
3
0
200
400
Time →

Fig. 3.45

$$X(t+1)-X(t) = aX(t) - bX(t)\,Y(t)$$
$$Y(t+1)-Y(t) = -cY(t) + dX(t-20)\,Y(t-20) \tag{48}$$

where X is the prey population and Y is the predator population.

Behaviour of the prey, predator population with respect to time is shown in Fig. 3.46 and Fig. 3.47 respectively. Fig. 3.48 shows mutual behaviour of prey-predator

in Sub Fig. 1 $a=.01$, $b=.002$, $c=.02$, $d=.001$

Sub Fig. 2 $a=.01$, $b=.004$, $c=.03$, $d=.002$

In both cases prey and Predators population will ~~increase~~ oscillate with time ~~while the predator population die out.~~ As the time increases. the amplitude of oscillation also increases

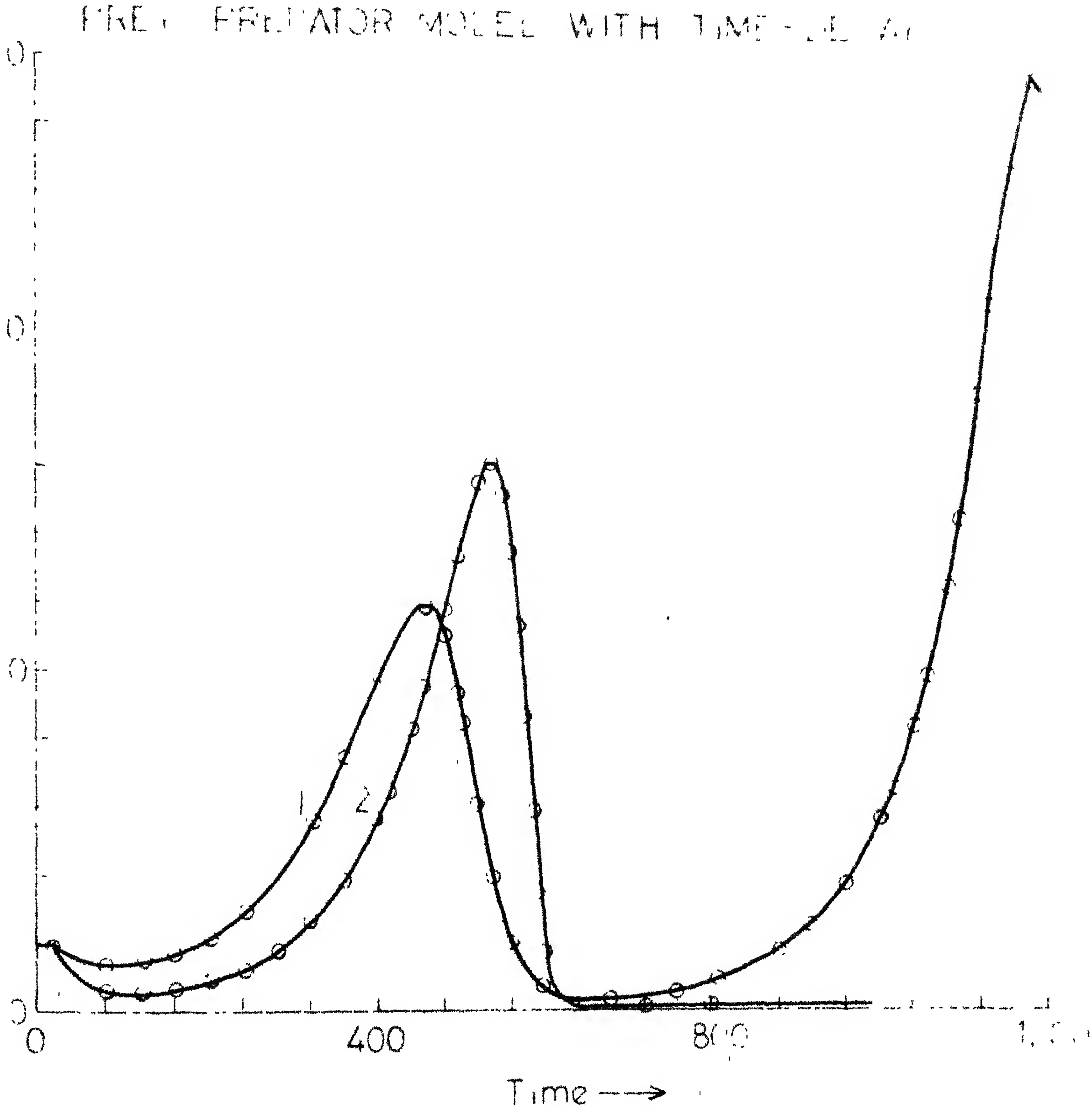


Fig 3.46

PREY - PREDATOR MODEL WITH TIME DELAY

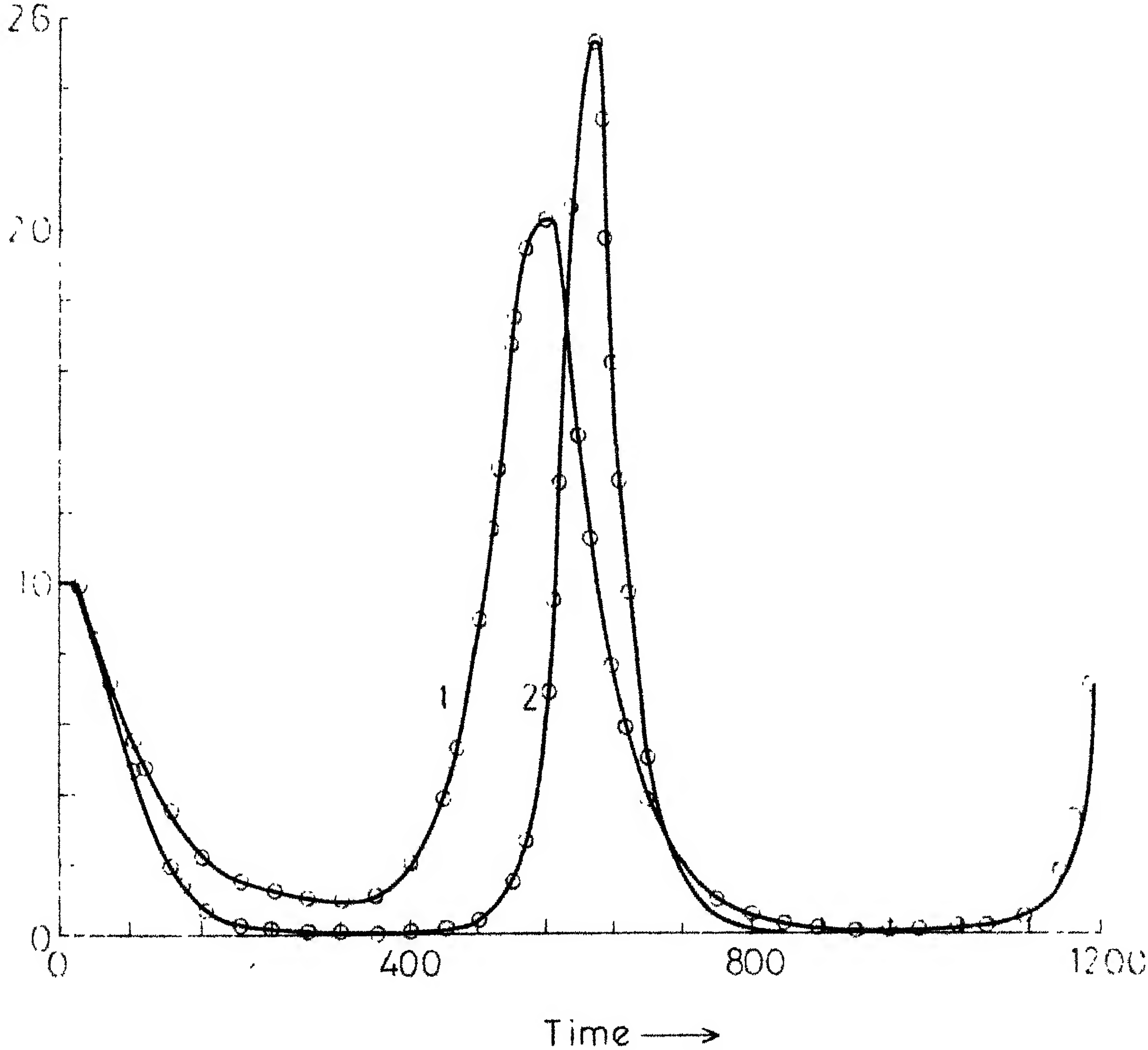
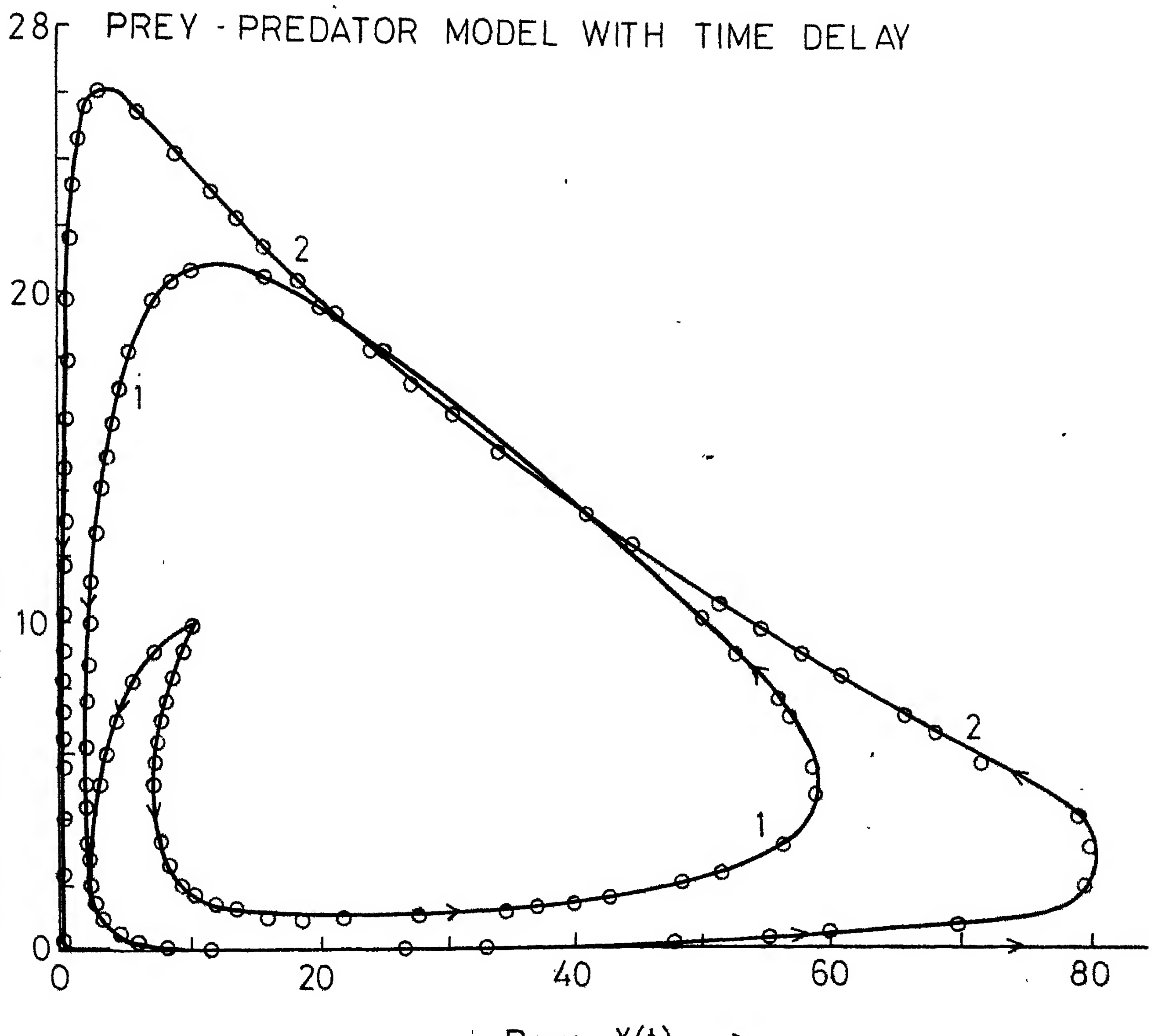


Fig. 3.47



28
PREY - PREDATOR MODEL WITH TIME DELAY
20
10
0
2
1
1
2
0
20
40
60
80
Prey X(t) ⟶

Fig. 3.48

CHAPTER - 4

RELATIVE STABILITY OF DIFFERENCE AND DIFFERENTIAL EQUATION SYSTEMS

4.1 INTRODUCTION

The choice between continuous and discrete population models from the point of view of stability has been discussed by a number of authors including Driessche [1974], Duffin [1969], Innes [1974], May [1973] and Usher [1969]. In particular May [1973] has considered the continuous model represented by

$$\frac{dN_j}{dt} = F_j[N_1(t), N_2(t)\ldots N_m(t)]; \; j=1,2,\ldots,m \tag{1}$$

and the analogous discrete model

$$N_j(t+1)-N_j(t) = F_j[N_1(t), N_2(t)\ldots N_m(t)]; \; j=1,2,\ldots,m \tag{2}$$

where $N_1(t), N_2(t),\ldots,N_m(t)$ are the populations of the m species and F_j's are non-linear interaction functions. For defining the analogous discrete system, May has replaced the derivative by a forward difference operator with step size $h > 0$ so that

$$\frac{d}{dt} N_j(t) \approx \frac{1}{h} (T-1) N_j, \tag{3}$$

where

$$TN_j(t) = N_j (t+h) \tag{4}$$

and time has been normalised so that $h = 1$.

In the two models, the biological features such as trophic structures, birth and death rates, competition and prey-predator interactions are identical. The equilibrium populations are also the same. The main difference is that while for (2), growth takes place in discrete steps, in (1) it is continuous process. May [1973] has stated that:

> ''It is widely understood that difference equations tend to be less stable than their differential equation twins, because the finite time lapse between generation of growth will have the destabilizing effects associated with any time lag in an interacting system. Our discussion makes it explicit, clearly stability of the difference equations system implies stability of the differential equation one, but the converse is not necessarily true''.

However Driessche [1974], using the operational rule

$$(T-1)\, N_j \approx \frac{h}{2}\,(T+1)\,\frac{dN_j}{dt} \qquad (5)$$

has shown that the resulting analogous discrete system is as stable as the differential equation system.

Here, we examine the operational rule

$$(T-1)N_j = \frac{h}{\rho+1}\,(1+\rho T)\,\frac{dN_j}{dt} \qquad (6)$$

where $\rho\,(\neq -1)$ is a parameter, to compare the stability of the continuous and discrete models. It is obvious that when

$\rho = 1$, (6) reduces to (5) and when $\rho = 0$, (6) reduces to (3), so that the results of Driessche (1974) and May (1973) should follow as particular cases of our results and we may expect to get additional insight by using other values of ρ.

4.2 ANALYTICAL DISCUSSION

Let $N_j^* \geq 0$, $(j = 1,2,\ldots,m)$ be the equilibrium population values, where

$$F_j\,(N_1^*, N_2^*, \ldots, N_m^*) = 0 \tag{7}$$

To discuss the stability of the equilibrium population, we perturb these by small disturbances $V_j(t)$ so that

$$N_j(t) = N_j^* \left[1 + V_j(t)\right] \quad (j=1,2,\ldots,m) \tag{8}$$

Substituting in (1), neglecting squares, products and higher powers of $V_j(t)$ and using (7), we get

$$\frac{dV_j}{dt} = \sum_{k=1}^{m} a_{jk}\, V_k(t), \qquad (j=1,2,\ldots,m) \tag{9}$$

where

$$a_{jk} = \frac{N_k^*}{N_j^*}\left(\frac{\partial F_j}{\partial N_k}\right)^* \tag{10}$$

and the partial derivative are evaluated at the equilibrium population values. Substituting

$$V_j(t) = B_j\, e^{\lambda t} \tag{11}$$

In (9), we find that this can be a solution provided

$$|A - \lambda I| = 0 \tag{12}$$

where A is the $m \times m$ matrix (a_{jk}). The system (1) will be stable if for all eigenvalues of A, we have

$$R_e \ \lambda < 0 \tag{13}$$

Substituting (8) in (6), we get

$$V_j(t+h) - V_j(t) = \frac{h}{\rho+1}(1+\rho T)\frac{dV_j}{dt} \tag{14}$$

using (9)

$$V_j(t+h)-V_j(t) = \frac{h}{\rho+1}\sum_{k=1}^{m} a_{jk}\{\rho V_k(t+h) + V_k(t)\}] \tag{15}$$

Substituting

$$V_j(t) = C_j \ \psi^t \tag{16}$$

we find that this will be a solution provided it satisfies the equation

$$|A - \frac{\rho+1}{h} \ \frac{\psi^h - 1}{\rho\psi^h+1} \ I| = 0 \tag{17}$$

The analogous discrete model will be stable if

$$|\psi| < 1 \tag{18}$$

4.3 GEOMETRICAL INTERPRETATIONS

Comparing (12) and (17) we get

$$\lambda = \frac{\rho+1}{h} \ \frac{\psi^h-1}{\rho\psi^h+1} \tag{19}$$

or

$$\psi^h = \frac{1+\rho+\lambda h}{1+\rho-\rho\lambda h} \tag{20}$$

The circular region $|\psi| < 1$ corresponds to the region

$$|1+\rho+\lambda h| < |1+\rho-\rho\lambda h|$$

or

$$(1+\rho+\lambda h)(1+\rho+\bar{\lambda}h) < (1+\rho-\rho\lambda h)(1+\rho-\rho h\bar{\lambda})$$

or

$$\lambda\bar{\lambda}\, h^2(1-\rho^2) + h(1+\rho)^2\, (\lambda+\bar{\lambda}) < 0$$

or

$$(X^2+Y^2)\,(1-\rho^2) + \frac{2X}{h}\,(1+\rho)^2 < 0 \qquad (21)$$

(i) If $|\rho| < 1$, (21) gives

$$(X+\frac{1}{h}\,\frac{1+\rho}{1-\rho})^2 + Y^2 < \frac{1}{h^2}\,(\frac{1+\rho}{1-\rho})^2 \qquad (22)$$

which is the interior of a circle with centre $(-\frac{1}{h}\,\frac{1+\rho}{1-\rho}, 0)$, radius $\frac{1}{h}\,\frac{1+\rho}{1-\rho}$ and which passes through the origin.

(ii) If $|\rho| > 1$, (21) gives

$$(X-\frac{1}{h}\,\frac{\rho+1}{\rho-1})^2 + Y^2 > \frac{1}{h^2}\,(\frac{\rho+1}{\rho-1})^2 \qquad (23)$$

which is the exterior of the circle with centre $(\frac{1}{h}\,\frac{\rho+1}{\rho-1}, 0)$ radius $\frac{1}{h}\,\frac{1+\rho}{\rho-1}$ and which passes through the origin.

(iii) If $\rho = 1$, (21) gives

$$X < 0 \qquad (24)$$

which is the left-hand half of the λ plane.

We show in Fig. 4.1, for different values of ρ, the regions corresponding to $|\psi| < 1$.

We get the following possibilities,

(i) When $\rho = 0$, we get the interior of the circle of

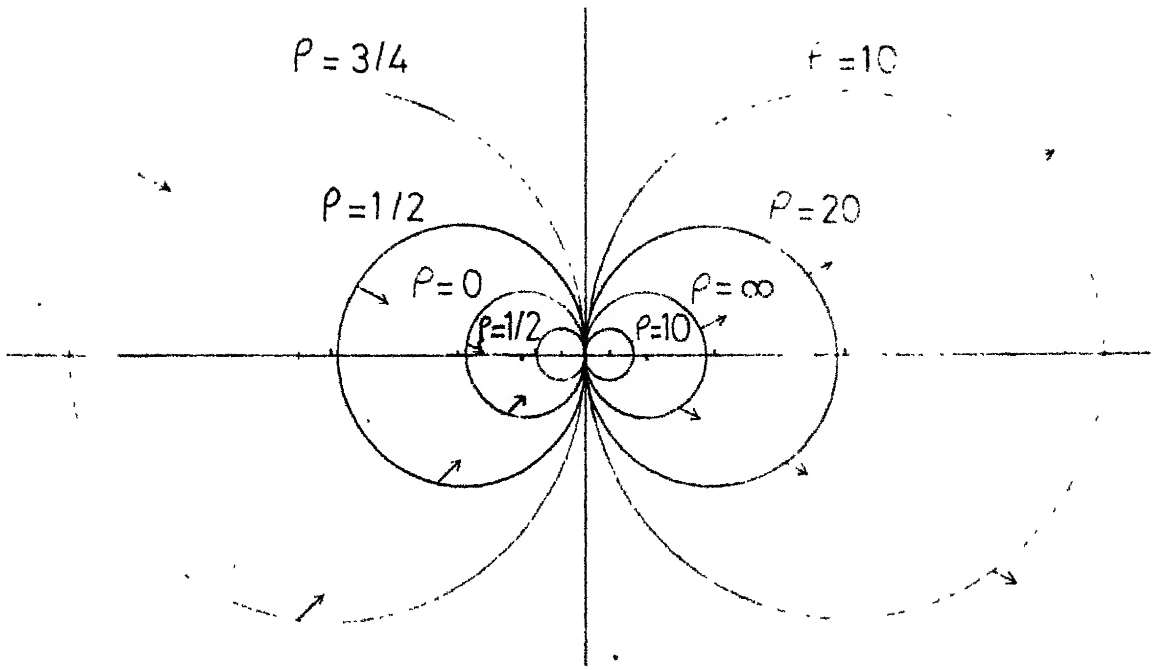


Fig. 4.1

centre $(-\frac{1}{h},0)$ and radius $\frac{1}{h}$. This corresponds to the case discussed by May [1973].

(ii) As ρ increases, we get interiors of larger and larger circles with centres on negative x-axis and all passing through the origin.

(iii) When $\rho = 1$, we get the whole of the left hand plane. This corresponds to the case discussed by Driessche [1974].

(iv) When $-1 < \rho < 0$, we get interiors of circles of radius less than $-\frac{1}{h}$ with centres on negative x-axis and passing through the origin. As $\rho \to -1 + 0$, we get just the point circle at the origin.

(v) When ρ is slightly greater than unity, we get the exterior of a large circle with centre on the positive x-axis and passing through the origin. This exterior includes the entire left hand half of the x-y plane and part of the right hand half of the x-y plane.

(vi) As ρ increases beyond unity, we get exteriors of smaller and smaller circles with centres on positive x-axis and passing through the origin.

(vii) A $\rho \to \infty$, we get the exterior of a circle of centre $(\frac{1}{h}, 0)$ and radius $\frac{1}{h}$.

(viii) When ρ in negative and large, we get the exterior of a circle of radius ~~larger~~ smaller than $\frac{1}{h}$, centre on the positive x-axis and passing through the origin.

(ix) As $\rho \to -1-0$, we get the circle of zero radius at the origin.

(x) As $h \to 0$, both the regions given by (22) and (23) approach the region $X < 0$ and in the limit both system tend to be equistable. This is of course expected.

4.4 COMPARISON OF THE STABILITY OF CONTINUOUS AND DISCRETE MODELS

Case I $-1 < \rho < 1$

In this case if the difference equation system is stable, $|\psi| < 1$ and the corresponding point in the λ-plane lies within the circle with centre $(-\frac{1}{h}\frac{1+\rho}{1-\rho}, 0)$ and radius $\frac{1}{h}\frac{1+\rho}{1-\rho}$ i.e. in the shaded region I so that $R_e \lambda < 0$ and the differential equation system is also stable.

On the other hand if the differential equation system is stable, $R_e \lambda < 0$ and the corresponding points lie in the left-hand half of the λ-plane, but this point can be outside shaded region I and $|\psi|$ can be greater than unity so that the difference equation can be unstable.

Thus in this case the stability of the difference equation system implies the stability of the differential equation system but the converse is not necessarily true.

Case II $\rho = 1$

In this case $|\psi| < 1 \implies R_e \lambda < 0$ and $R_e\lambda < 0 \implies |\psi| < 1$ so that the two systems are both stable or both unstable. This is the case discussed by Driessche [1974].

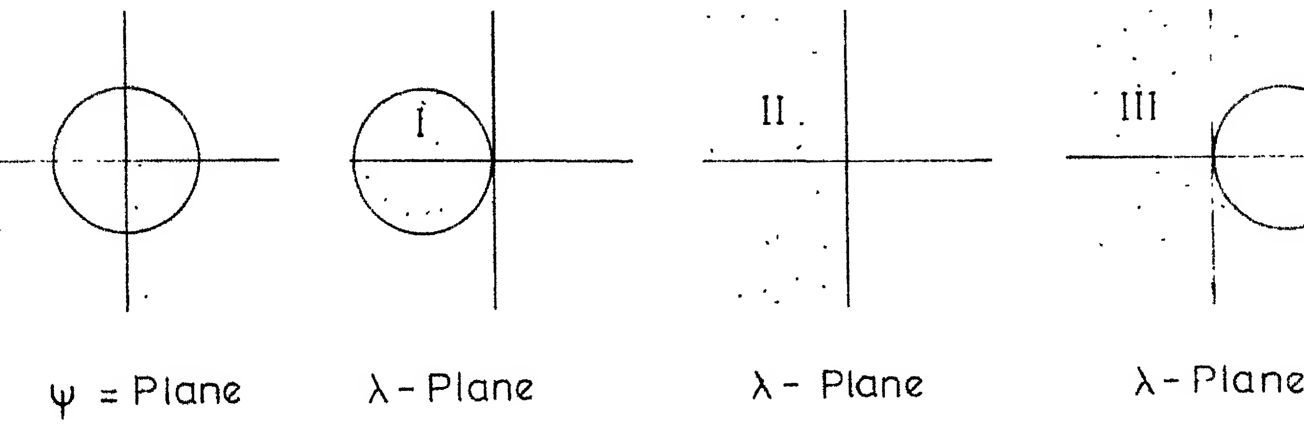


Fig. 4.2

Case III $|\rho| > 1$

In this case the region $|\psi| < 1$ corresponds to the region III in the λ plane. When $|\psi| < 1$, $R_e\ \lambda$ may be positive or negative. Thus $R_e \lambda < 0 \Longrightarrow |\psi| < 1$, but $|\psi| < 1 \not\Longrightarrow R_e\ \lambda < 0$ so that the stability of the differential equation system implies the stability of the difference equation system, but the converse is not necessarily true.

4.5 DISCUSSION

We have shown that the relative stability of the difference and differential equations models depends on the operator used and we have demonstrated an operator for which difference equation model is actually more stable.

When $\rho < 1$, difference equation model is less stable, but by making h smaller and smaller, we can make region of stability larger and larger till it coincides with the region of stability for the differential equation.

When $\rho > 1$, differential equation is less stable, but again by making h smaller and smaller, we can make its region of stability larger and larger till it coincides with the region of stability of the difference equation.

When $\rho = 1$, the region of stability is the same for all small values of h.

This discussion is illustrated with an age-structured population model with three age-groups.

4.6 AN AGE-STRUCTURED POPULATION MODEL

We divide the population into three groups, the pre-reproductive, the productive and the post-reproductive. Let d_1, d_2, d_3 be the death rates in the three groups and b_2 be the birth rate in the reproductive group. Also let m_1, m_2 be the rates at which individual from first and second groups migrate to second and third groups respectively, then the basic differential equation for the model are

$$\begin{aligned} \frac{dX_1}{dt} &= b_2X_2 - (d_1+m_1)X_1 \\ \frac{dX_2}{dt} &= m_1X_1 - (d_2+m_2)X_2 \\ \frac{dX_3}{dt} &= m_2X_2 - d_3X_3 \end{aligned} \tag{25}$$

or

$$\frac{dX}{dt} = AX \tag{26}$$

where

$$X(t) = \begin{bmatrix} X_1(t) \\ X_2(t) \\ X_3(t) \end{bmatrix}, \quad A = \begin{bmatrix} -(d_1+m_1) & b_2 & 0 \\ m_1 & -(d_2+m_2) & 0 \\ 0 & m_2 & -d_3 \end{bmatrix}$$

The eigenvalues of A are given by

$$\begin{aligned} \lambda_1, \lambda_2 &= \frac{1}{2}\{-(d_1+m_1+d_2+m_2) \pm [(d_1+m_1+d_2+m_2)^2 - 4(d_1+m_1)(d_2+m_2)+4b_2m_1]^{1/2}\} \\ &= \frac{1}{2}\{-(d_1+m_1+d_2+m_2) \pm [(d_1+m_1-d_2-m_2)^2 + 4b_2m_1]^{1/2}\} \end{aligned} \tag{27}$$

(28)

All roots are real. Two roots are negative and the third is negative or positive according as

$$(d_1+ m_1)\ (d_2+ m_2)\ \gtrless b_2 m_1 \tag{29}$$

Thus the equilibrium position (0,0,0) for the model (25) would be stable if

$$(d_1+ m_1)\ (d_2+ m_2) > b_2 m_1 \tag{30}$$

and it would be unstable if

$$(d_1+ m_1)\ (d_2+ m_2) < b_2 m_1 \tag{31}$$

For this model, all the eigenvalues are real and therefore we discuss in the next section, the relative stability of differential and difference equation model for the special case when the eigenvalues of the differential equation model are real.

4.7 RELATIVE STABILITY OF DIFFERENTIAL AND DIFFERENCE EQUATION SYSTEMS WHEN λ IS REAL

From (20), $$\psi^h = \frac{1+\rho+\lambda h}{1+\rho-\rho\lambda h} = \frac{1+\rho+K}{1+\rho-\rho K}\ , \quad K = \lambda h \tag{32}$$

Case 1 $\quad \lambda > 0, \quad \lambda h = K > 0$

Consider the curve

$$y = \frac{1+x+K}{1+x-Kx} \quad , \quad 0 < K < 1 \tag{33}$$

When $X = 0$, $y = 1+K > 1$

when $X \to \pm \infty$, $Y \to \frac{1}{1-K} > 1+K$

when $X \to \frac{-1}{1-K} \mp 0$, $Y \to \pm \infty$

The curve has two asymptates

$$X = -\frac{1}{1-K}\ ,\ Y = \frac{1}{1-K}$$

when $Y = 0,\ X = -(1+K)$

when $Y = 1,\ X = -1$

when $Y = -1,\ X = -\frac{2+K}{2-K}$

If $-\frac{2+K}{2-K} < X < -1$, then $-1 < Y < 1$ (34)

If $-\frac{2+\lambda h}{2-\lambda h} < \rho < -1$, then $-1 < \psi^h < 1$ or $|\psi| < 1$ (35)

If $\rho > -1$ or $\rho < -\frac{2+\lambda h}{2-\lambda h}$, then $|\psi| > 1$ (36)

The curve sketched is shown in Fig. 4.3

<u>Case II</u> $\lambda < 0,\ \lambda h = -k,\ k > 0$

We consider the curve

$$Y = \frac{1+x-k}{1+x+kx}\ ,\quad 0 < k < 1 \tag{37}$$

Proceeding as above, we get the curve sketched in Figure 4.4

When $-1 < X < -\frac{2+\lambda h}{2-\lambda h}$, $|Y| > 1$

When $-1 < \rho < -\frac{2+\lambda h}{2-\lambda h}$, $|\psi| > 1$

when $\rho < -1$ or $\rho > -\frac{2+\lambda h}{2-\lambda h}$, $|\psi| < 1$.

Thus we get the situation represented in the Figure 4.5

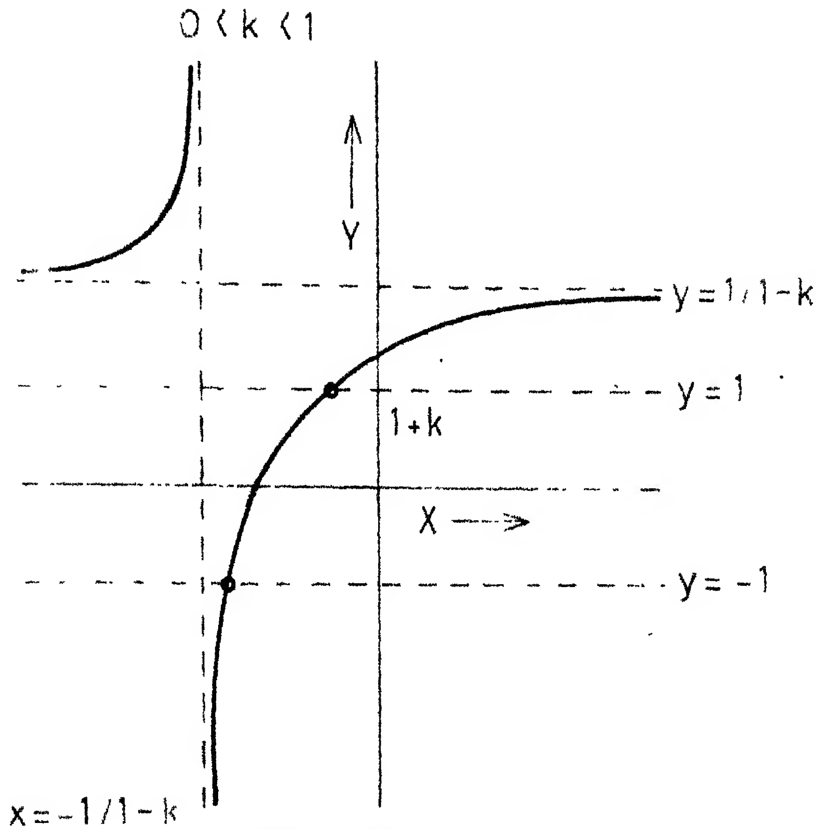


Fig 4.3

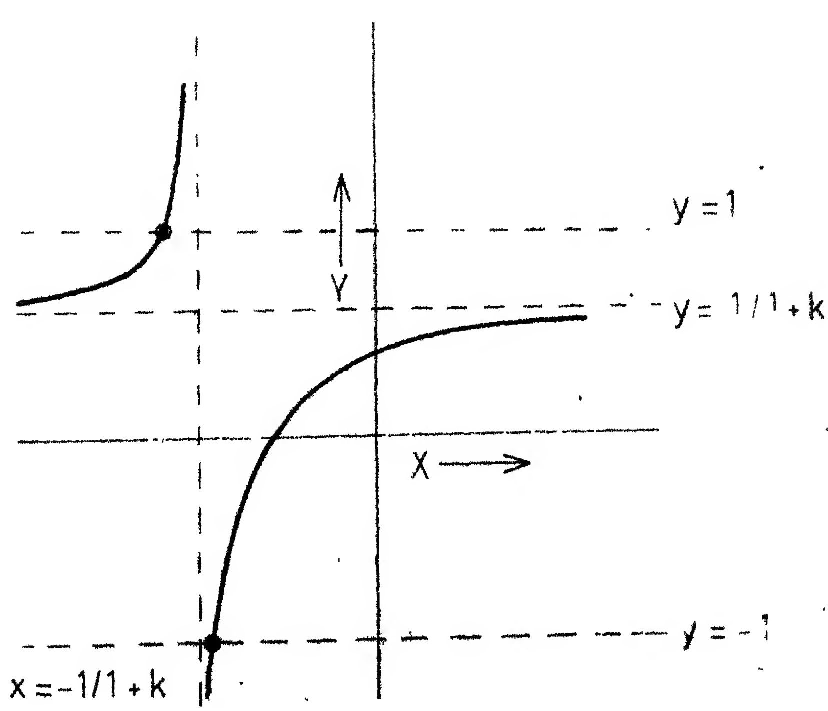


Fig.4.4

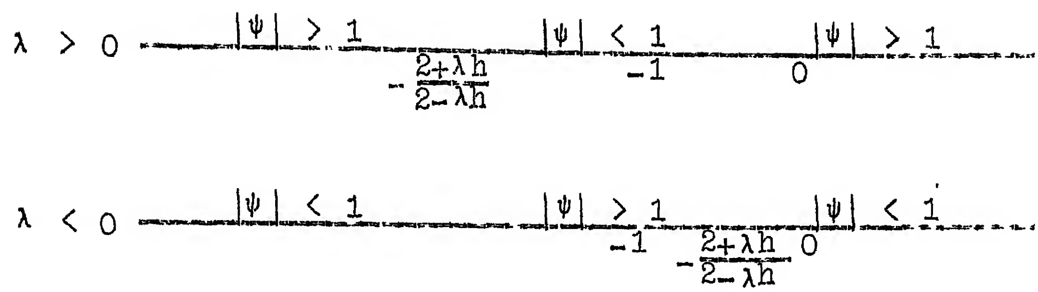


Figure 4.5

Thus when λ is real, we get the following results

(i) When $\rho < \min\left(-1, -\frac{2+\lambda h}{2-\lambda h}\right)$ or $\rho > \max\left(-1, -\frac{2+\lambda h}{2-\lambda h}\right)$, either both models are stable or both are unstable.

(ii) When ρ lies between -1 and $-\frac{2+\lambda h}{2-\lambda h}$, one model is stable and the other is unstable.

Thus when λ is real, we find that when ρ lies between -1 and $-\frac{2+\lambda h}{2-\lambda h}$, either $\lambda > 0$ and $|\psi| < 1$ or $\lambda < 0$ and $|\psi| > 1$.

4.8 <u>EXAMPLE OF AGE-STRUCTURED POPULATION MODEL</u>

<u>Case 1</u> $b_2 m_1 > (d_1+m_1)(d_2+m_2)$

There are three eigen values $-\lambda_1, -\lambda_2, \lambda_3$ where $\lambda_1, \lambda_2, \lambda_3 > 0$.

If ρ is taken between $-\frac{2+\lambda_3 h}{2-\lambda_3 h}$ and -1, $|\psi_1| < 1$, $|\psi_2| < 1$, $|\psi_3| < 1$.

In this case the differential equation model is unstable and the difference equation model is stable. For other values of ρ, both models are unstable.

<u>Case II</u> $b_2 m_1 < (d_1+m_1)(d_2+m_2)$

Here the three eigenvalues are $-\lambda_1$, $-\lambda_2$, $-\lambda_3$ $(\lambda_1, \lambda_2, \lambda_3 > 0)$.

If ρ is taken in the intersection of the interval

$$\left(-\frac{2-\lambda_1 h}{2+\lambda_1 h}, -1\right), \left(-\frac{2-\lambda_2 h}{2+\lambda_2 h}, -1\right), \left(-\frac{2-\lambda_3 h}{2+\lambda_3 h}, -1\right)$$

then $|\psi_1| > 1$, $|\psi_2| > 1$, $|\psi_3| > 1$.

In this case the diffrential equation is stable and the difference equation model is unstable. For other values of ρ, both models would be stable.

The smaller h is, the smaller is the interval for exceptional values of ρ for which both models behave differently. When $h \to 0$, both models are stable or unstable.

CHAPTER - 5

BIFURCATION THEORY FOR TWO POPULATION MODELS

5.1 INTRODUCTION

Bifurcation theory is a study of the branching of solutions of nonlinear differential equation. It is of particular interest in bifurcation theory to study how the solutions and their multiplicity changes as parameters vary. Thus at a bifurcation point there is a transition in solution multiplicity. Application of Bifurcation theory are in elastic and hydrodynamic stability. In elastic stability theory, bifurcation is called buckling. In hydrodynamic stability, bifurcation points are called transition or critical points.

Bifurcation theory, known as branching theory as a mathematical discipline, had its origin towards the end of 19th century, in the work of Poincare (1892-99) who made use of nonlinear perturbation theory in celestial mechanics and who was followed by Liapunov [1906] and Schmidt [1910] who, in turn worked in the area of nonlinear integral equations, and then, in late twenties by Hildebrandt and Graves [1927] provided an essential step in the development of bifurcation theory.

Important developments were made by the Soviet school of Krasnoselskü [1964] and Vainberg [1968] and significant growth

was experienced in the sixties. The basic mathematical ideas are contained in the book of Pimbley [1969] while numerous physical applications can be found in the book edited by Keller and Antaman [1969]. Bifurcation theory made significant progress and has find application in various established fields and to many new and emerging sciences. Bifurcation theory has been widely acclaimed and has found fruitful applications in theoretical biology.

J.F.G. Auchmuty and G. Nicolis [1975] using bifurcation theory constructed new steady state solutions of a nonlinear network involving chemical reaction and diffusion. Same authors in [1976] described oscillator solutions of a system of reaction-diffusion equations. Here solutions exist for a wide range of values of the parameters and may be calculated by using the technique of bifurcation theory. M. Herschkowitz-Kaufman [1975] made a detailed comparison for different boundary conditions between the analytical solution of the Kinetic equations obtained by bifurcation theory and the results of computer simulations. W.H. Fleming's [1975] models on genetics, deal with selection migration and his result concern the existence and stability properties and bifurcation phenomena for equulibrium solutions. J. Guckenheimer and G. Oster [1977] studied dynamics of density-dependent population models. They illustrated the general theory on a density-dependent Leslie model with two age classes. The pattern of

bifurcation away from the equilibrium point was investigated. Yieh Hei-Wan [1978] used two methods to study stability criterion for the Hopf bifurcation of diffeomorphisms on $\mathbb{R}^2$. The formula was then applied to the study of a density dependent Leslie model of two age classes. George H. Pimbley [1974] in a predator-prey model shows that for certain parametric values there exist a closed separatrix in the phase plane and gave conditions under which this closed sepratrix is stable or unstable. Then he used bifurcation theorem of Andronov and Leontovich to show how larger amplitude periodic solutions branch from this closed sepratrix. J.F. Perez [1978] discussed population oscillations in isolated populations of flies. He analyzed the solutions in terms of the parameter range. He found a condition which shows that a pair of root crosses the imaginary axis a single time. Each time a pair of roots crosses the imaginary axis; qualitative changes are expected in the solutions where this occurs. This is called Hopf bifurcation. J.M. Cushing [1976] considered a general integrodifferential system which described a predator-prey interaction subject to delay effects. He shows that there are critical values of birth and death of prey and predator at which stable periodic solution bifurcate from the equilibrium. He does not consider the stability of the bifurcating periodic solutions. The problem of determining the stability of a non-

constant periodic solution is in general quite difficult for integrodifferential systems(and even for ordinary differential systems). In this regard MacDonald [1977] considered the bifurcation of periodic solutions for a $n=2$ predator-prey model with delays. Mac Donald's approach is to convert the integrodifferential system to a larger differential system and then apply Hopf bifurcation techniques. These results of Mac Donald for predator-prey model are analytically obtained stability results for the bifurcating periodic solutions of integrodifferential systems. J.M. Cushing [1977a] asserts the existence of nonconstant periodic solution which bifurcate from equilibrium as certain parameters pass through critical values. J.M. Cushing [1977b] modifed predator-prey dynamics represented by differential equations by the assumption that the coefficients are periodic function of times. By using bifurcation theory he has shown that this system has a periodic solution. Numerical results which clearly show this bifurcation phenomena are briefly discussed. In the present chapter, a set of conditions for a pair of eigenvalues of a stability problem matrix to be purely imaginary are obtained for a general physical system. These conditions are then applied to discuss the existence of bifurcation points for (i) time-delay prey-predator model and (ii) growth of a single population under the effect of pollution.

5.2 DETERMINATION OF POINTS OF BIFURCATION A GENERAL STABILITY THEORY

Consider a physical system governed by the system of differential equations

$$\frac{dX_i}{dt} = f_i(X_1, X_2, \ldots, X_n,\ C_1, C_2, \ldots, C_m) \quad (i=1,2,\ldots,n) \qquad (1)$$

where $C_1, C_2, \ldots, C_m$ are certain parameters.

Its equilibrium points are given by

$$f_i(X_1, X_2, \ldots, X_n,\ C_1, C_2, \ldots, C_m) = 0 \quad (i=1,2,\ldots,n) \qquad (2)$$

Let $(\hat{X}_1, \hat{X}_2, \ldots, \hat{X}_n)$ be an equilibrium point.

let $$X_i = \hat{X}_i + u_i \qquad (i=1,2,\ldots,n) \qquad (3)$$

Substituting in (1), using (2) and neglecting squares, products and higher power of u_i's, we get

$$\frac{du_i}{dt} = \sum_{j=1}^{n} \frac{\partial f_i}{\partial X_j} u_j = \sum_{j=1}^{n} a_{ij} u_j \ \text{(say)} \quad (i=1,2,\ldots,n) \qquad (4)$$

Substituting

$$u_i = A_i e^{\lambda t} \qquad (i=1,2,\ldots,n) \qquad (5)$$

we find that (5) will give a solution of (4) if

$$|A - \lambda I| = 0 \qquad (6)$$

where A is the matrix

$$\begin{bmatrix} a_{11} & a_{12} & \cdots\cdots & a_{1n} \\ a_{21} & a_{22} & \cdots\cdots & a_{2n} \\ \cdots & \cdots & \cdots\cdots & \cdots \\ \cdots & \cdots & \cdots\cdots & \cdots \\ a_{n1} & a_{n2} & \cdots\cdots & a_{nn} \end{bmatrix} \qquad (7)$$

Let eqn. (6) be written as

$$\lambda^n + K_1\lambda^{n-1} + K_2\lambda^{n-2} + \ldots + K_n = 0 \qquad (8)$$

where $K_1, K_2, \ldots, K_n$ are functions of the parameters $C_1, C_2, \ldots, C_m$. For discussing bifurcation, we are interested in finding whether (7) or (8) can have purely imaginary roots of the form $\pm i\omega$. The interest arises because the nature of the equilibrium point changes when parameter values change slightly in this case. For the two dimensional case if the roots are $V \pm i\omega$, we get an unstable focus if $V > 0$, a centre if $V = 0$ and a stable node if $V < 0$. V is a function of the parameters and for some values of the parameters, V can be zero. A slight change in the values of the parameters would change the nature of the equilibrium.

If $\pm i\omega$ are roots of (8), we get

$$(\omega^n - K_2\omega^{n-2} + K_4\omega^{n-4} - \ldots) \pm i(K_1\omega^{n-1} - K_3\omega^{n-3} + \ldots) = 0 \quad (9)$$

Equating real and imaginary parts seperately to zero, we get

$$\omega^n - K_2\omega^{n-2} + K_4\omega^{n-4} - \dots + (-1)^{(n-1)/2} K_{n-1}\,\omega = 0$$
$$K_1\omega^{n-1} - K_3\omega^{n-3} + K_5\omega^{n-5} - \dots + (-1)^{(n-1)/2} K_n = 0 \tag{10}$$

if n is odd and

$$\omega^n - K_2\omega^{n-2} + K_4\omega^{n-4} \dots\dots (-1)^{n/2} K_n = 0$$
$$K_1\omega^{n-1} - K_3\omega^{n-3} + K_5\omega^{n-5} \dots\dots (-1)^{(n-2)/2} K_{n-1}\omega = 0 \tag{11}$$

is n is even.

For (8) to have a pair of purely imaginary roots, equations (10) or (11) should have a common real solution.

2. SPECIAL CASES*

For $n = 2$

$$\omega^2 - K_2 = 0, \; K_1\omega = 0 \tag{12}$$

The required conditions are

$$K_1 = 0, \; K_2 > 0 \tag{13}$$

For $n = 3$

$$\omega^3 - K_2\,\omega = 0, \; K_1\omega^2 - K_3 = 0 \tag{14}$$

The required conditions are

$$K_2 > 0, \; \frac{K_3}{K_1} > 0, \quad K_2 = \frac{K_3}{K_1} \tag{15}$$

For $n = 4$

$$\omega^4 - K_2\omega^2 + K_4 = 0, \; K_1\omega^3 - K_3\,\omega = 0 \tag{16}$$

The required conditions are

$$\frac{K_3}{K_1} > 0, \; K_3^2 - K_1K_2K_3 + K_4K_1^2 = 0 \tag{17}$$

For $n = 5$

$$\omega^5 - K_2\omega^3 + K_4\,\omega = 0, \quad K_1\omega^4 - K_3\omega^2 + K_5 = 0 \tag{18}$$

or

$$\frac{\omega^4}{K_3K_4-K_2K_5} = \frac{\omega^2}{K_4K_1-K_5} = \frac{1}{K_1K_2-K_3}$$

The required conditions are

$$\frac{K_4K_1-K_5}{K_1K_2-K_3} > 0 \tag{19a}$$

$$(K_1K_4-K_5)^2 = (K_3K_4-K_2K_5)(K_1K_2-K_3) \tag{19b}$$

for $n = 6$

$$\omega^6 - K_2\omega^4 + K_4\omega^2 - K_6 = 0, \quad K_1\omega^5 - K_3\omega^3 + K_5\,\omega = 0 \tag{20}$$

These give

$$K_3\omega^4 - \omega^2\,(K_2K_3+K_5-K_1K_4) + K_2K_5-K_1K_6 = 0$$

and

$$K_1\omega^4 - \omega^2K_3 + K_5 = 0$$

or

$$\frac{\omega^4}{K_3(K_2K_5-K_1K_6)-K_5(K_2K_3+K_5-K_1K_4)} = \frac{\omega^2}{K_1(K_2K_5-K_1K_6)-K_3K_5}$$

$$= \frac{1}{K_1(K_2K_3+K_5-K_1K_4)-K_3^2}$$

The required conditions are

$$\frac{K_1K_2K_5 - K_1^2 K_6 - K_3K_5}{K_1K_2K_3 + K_1K_5 - K_1^2K_4 - K_3^2} > 0 \tag{21a}$$

and

$$(K_1K_2K_5 - K_1^2K_6 - K_3K_5)^2 = (K_1K_4K_5 - K_3K_1K_6 - K_5^2) \times (-K_3^2 + K_1K_2K_3 + K_1K_5 - K_1^2K_4) \tag{21b}$$

For $n = 7$

$$\omega^7 - K_2\,\omega^5 + K_4\,\omega^3 - K_6\,\omega = 0 \tag{22a}$$

$$K_1\,\omega^6 - K_3\,\omega^4 + K_5\,\omega^2 - K_7 = 0 \tag{22b}$$

These give

$$(-K_3 + K_1K_2)\,\omega^4 + (K_5 - K_1K_4)\,\omega^2 - (K_7 - K_6K_1) = 0 \tag{23a}$$

and

$$\omega^4\left[K_5 - K_1K_4 + K_1K_2^2 - K_2K_3\right] - \omega^2\left[K_7 - K_6K_1 + K_1K_2K_4 - K_3K_4\right] + (K_6K_1K_2 - K_6K_3) = 0 \tag{23b}$$

The required conditions are

$$\frac{K_6K_1K_5 - K_1^2K_6K_4 + K_1K_4K_7 - K_5K_7 - K_1K_2^2K_7 + K_2K_3K_7 + K_1K_2K_3K_6 - K_3^2K_6}{K_3K_7 - K_3K_6K_1 - K_3^2K_4 + K_1K_2K_3K_4 + K_1^2K_2K_6 - K_1K_2K_7 - K_5^2 - K_1K_2^2K_5 + K_2K_3K_5 - K_1^2K_4^2 + 2K_1K_4K_5} > 0 \tag{24a}$$

and

$$\begin{aligned}
&(K_6K_1K_5-K_1^2K_6K_4-K_5K_7-K_1K_2^2K_7+K_2K_3K_7+K_1K_2K_3K_6-K_3^2K_6+K_1K_4K_7)^2 \\
&=(K_1K_2K_6K_5-K_3K_6K_5-K_6^2K_1^2+2K_1K_6K_7-K_7^2+K_3K_4K_7-K_1K_2K_4K_7) \\
&\quad(-K_3K_6K_1+K_3K_7-K_3^2K_4+K_1K_2K_3K_4+K_1^2K_2K_6-K_1K_2K_7 \\
&\quad-K_5^2+2K_1K_4K_5-K_1K_2^2K_5+K_2K_3K_5-K_1^2K_4^2) \qquad (24b)
\end{aligned}$$

Thus we find that in every case we get two conditions. One of which is an inequality and other is an equation. The second condition involves $C_1, C_2, \ldots, C_m$. If $(m-1)$ of the parameters are kept fixed, this will determine the value of the mth parameter. If the value of this parameter is changed slightly from this value, the nature of the equilibrium will change, although the first condition will continue to be satisfied.

5.3 TIME-DELAY PREDATOR-PREY MODELS

The prey-predator model where interaction among them depend upon the current values is given by

$$\frac{dN}{dt} = f(N,P)$$
$$\frac{dP}{dt} = g(N,P) \qquad (25)$$

where N,P are the numbers of prey predators respectively. Growth rate of predators will depend not only on what they eat to-day but also on the past history for the growth of predators, then N in the second equation of (25) can be replaced by

$$Q(t) = \int_{-\infty}^{t} N(T)\, G(t-T)\,dT \tag{26}$$

where the kernal function $G(t-T)$ gives the effect of eating one prey by predator at time T after the time interval $(t-T)$. This gives an integrodifferential equation. Time-delay predator-prey models have been discussed by Wangersky and Cunningham [1957] and MacDonald [1976, 1977] in particular. To solve this integrodifferential equation MacDonald [1977] considered the special case

$$G(z) = a^r z^{r-1} e^{-az} \Gamma(r)^{-1} \tag{27}$$

Let

$$Q_1(t) = \int_{-\infty}^{t} \frac{N(T)a^r (t-T)^{r-1} e^{-a(t-T)}}{\Gamma(r)}\,dT \tag{28}$$

Differentiating equation (28) with respect to time

$$\frac{dQ_1}{dt} = \int_{-\infty}^{t} \frac{N(T)a^r (r-1)(t-T)^{r-2} e^{-a(t-T)}}{\Gamma(r)}\,dT - \int_{-\infty}^{t} \frac{N(T)a^{r+1}(t-T)^{r-1} e^{-a(t-T)}}{\Gamma(r)}\,dT$$

$$= a(Q_2 - Q_1) \tag{29}$$

similarly we can write

$$\frac{dQ_i}{dt} = a(Q_{i+1} - Q_i) \tag{30}$$

Now

$$Q_r(t) = \int_{-\infty}^{t} N(T)\, a\, e^{-a(t-T)}\,dT \tag{31}$$

on differentiating with respect to time

$$\frac{dQ_r}{dt} = \int_{-\infty}^{t} N(T)\, a^2 e^{-a(t-T)} dT + aN(t)$$

$$= a(N-Q_r) \qquad (32)$$

In this way one may write an ordinary differential equation of r^{th} order for Q, so that the equations (25), are replaced by system of differential equations given below

$$\frac{dN}{dt} = f(N,P)$$

$$\frac{dP}{dt} = g(Q_1,P)$$

$$\frac{dQ_i}{dt} = a(Q_{i+1}-Q_i) \qquad (33)$$

$$\frac{dQ_P}{dt} = a(N-Q_P)$$

writing precisely the equation (33)

$$\frac{dN}{dt} = \epsilon N(1 - \frac{N}{K}) - \alpha NP$$

$$\frac{dP}{dt} = -\gamma P + \beta P Q_1 \qquad (34)$$

$$\frac{dQ_i}{dt} = a(Q_{i+1}-Q_i) \qquad (i=1,2,\ldots,r-1)$$

$$\frac{dQ_r}{dt} = a(N-Q_r)$$

Making the substitution

$$N = Kn,\ P = Kp,\ Q = Kq\ ,\ \tau = \epsilon t \qquad (35)$$

we get

$$\begin{aligned} \dot{n} &= n(1-n) - bnp \\ \dot{p} &= -cp + dpq_1 \\ \dot{q}_i &= f(q_{i+1} - q_i) \\ \dot{q}_r &= f(n-q_r) \end{aligned} \tag{36}$$

where

$$b = \frac{K\alpha}{\epsilon}\ , \quad c = \frac{\gamma}{\epsilon}\ , \quad d = \frac{K\beta}{\epsilon}\ , \quad f = \frac{a}{\epsilon} \tag{37}$$

The matrix A for this system is given by

$$\begin{bmatrix} -n^* & -bn^* & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & dp^* & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & -f & f & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & -f & f & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & -f & \cdots & 0 & 0 \\ \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdots & \cdot\cdot & \cdot\cdot \\ 0 & 0 & 0 & 0 & 0 & \cdots & -f & f \\ f & 0 & 0 & 0 & 0 & \cdots & 0 & -f \end{bmatrix} \tag{38}$$

The equation for eigenvalues on simplification, gives

$$\begin{aligned} \lambda^{r+2} &+ \lambda^{r+1}({}^rC_1 f + n^*) + \lambda^r({}^rC_2 f^2 + n^*\,{}^rC_1 f) \\ &+ \lambda^{r-1}({}^rC_3 f^3 + n^*\,{}^rC_2 f^2) + \cdots \\ &+ \lambda^2 (f^r + n^*\,{}^rC_1 f^{r-1}) + \lambda n^* f^r + \alpha f^r = 0 \end{aligned} \tag{39}$$

where

$$n^* = q_1^* = q_2^* = \cdots = q_r^* = \frac{c}{d},\ p^* = \frac{d-c}{db},\ \alpha = \frac{c}{d}(d-c) \tag{40}$$

we get

$$\begin{aligned}
\dot{n} &= n(1-n) - bnp \\
\dot{p} &= -cp + dpq_1 \\
\dot{q}_i &= f(q_{i+1} - q_i) \\
\dot{q}_r &= f(n-q_r)
\end{aligned} \tag{36}$$

where

$$b = \frac{K\alpha}{\epsilon}\ , \ c = \frac{\gamma}{\epsilon}\ , \ d = \frac{K\beta}{\epsilon}\ , \ f = \frac{a}{\epsilon} \tag{37}$$

The matrix A for this system is given by

$$\begin{bmatrix}
-n^* & -bn^* & 0 & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & dp^* & 0 & 0 & \cdots & 0 & 0 \\
0 & 0 & -f & f & 0 & \cdots & 0 & 0 \\
0 & 0 & 0 & -f & f & \cdots & 0 & 0 \\
0 & 0 & 0 & 0 & -f & \cdots & 0 & 0 \\
\cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdot\cdot & \cdots & \cdot\cdot & \cdot\cdot \\
0 & 0 & 0 & 0 & 0 & \cdots & -f & f \\
f & 0 & 0 & 0 & 0 & \cdots & 0 & -f
\end{bmatrix} \tag{38}$$

The equation for eigenvalues on simplification, gives

$$\begin{aligned}
&\lambda^{r+2} + \lambda^{r+1}\,({}^rC_1 f + n^*) + \lambda^r\,({}^rC_2 f^2 + n^*\,{}^rC_1 f) \\
&\quad + \lambda^{r-1}\,({}^rC_3 f^3 + n^*\,{}^rC_2 f^2) + \cdots \\
&\quad + \lambda^2\,(f^r + n^*\,{}^rC_1 f^{r-1}) + \lambda n^* f^r + \alpha f^r = 0
\end{aligned} \tag{39}$$

where

$$n^* = q_1^* = q^*_2 = \cdots = q_r^* = \frac{c}{d},\ p^* = \frac{d-c}{db},\ \alpha = \frac{c}{d}\,(d-c) \tag{40}$$

5.4 SPECIAL CASES

(i) $r = 1$

$$\lambda^3 + \lambda^2 (f + n^*) + \lambda n^* f + \alpha f = 0 \tag{41}$$

(ii) $r = 2$

$$\lambda^4 + \lambda^3(2f+n^*) + \lambda^2(f^2+2n^*f) + \lambda n^*f^2 + \alpha f^2 = 0 \tag{42}$$

(iii) $r = 3$

$$\lambda^5 + \lambda^4(3f+n^*) + \lambda^3(3f^2+3n^*f) + \lambda^2(f^3+3n^*f^2) + \lambda n^*f^3 + \alpha f^3 = 0 \tag{43}$$

(iv) $r = 4$

$$\lambda^6 + \lambda^5(4f+n^*) + \lambda^4(6f^2+4n^*f) + \lambda^3(4f^3+6n^*f^2) + \lambda^2(f^4+4n^*f^3) + \lambda n^*f^4 + \alpha f^4 = 0 \tag{44}$$

For discussing the existence of points of bifurcation, we apply the conditions (15), (17), (19) and (21).

For $r = 1$ the required condition is

$$f = \frac{d^2-dc-c}{d} \tag{45}$$

Thus for a bifurcation point to exist, we should have

$$d^2 > (d+1)c \tag{46}$$

For $r=2$, the required condition is

$$-2n^*f^3+f^2(4\alpha-4n^{*2})+f(4n^*\alpha-2n^{*3}) + \alpha n^{*2} = 0 \tag{47}$$

This equation does have a positive real root and as such in this case, a bifurcation point does exist.

For $r = 3$, the required conditions are

$$\frac{n^*f^3(3f + n^*) - \alpha f^3}{(3f+n^*)(3f^2+3n^*f) - (f^3+3n^*f^2)} > 0 \tag{48}$$

and or $\alpha < n^*(3f + n^*)$

$$-8n^*f^4+f^3(24\alpha-24n^{*2}) + f^2(-24n^{*3}+ 45\,\alpha n^*)$$
$$+f(-8n^{*4}+34\alpha n^{*2}+\alpha^2) + 9\alpha n^{*3} = 0 \tag{49}$$

Equation (49) has at least one real positive root. If this satisfies eqn. (48), a point of bifurcation exists.

For $r=4$, the required conditions are

$$\frac{(4f+n^*)(6f^2+4n^*f)(n^*f^4)-(4f+n^*)^2\alpha f^4-(4f^3+6n^*f^2)n^*f^4}{(4f+n^*)(6f^2+4n^*f)(4f^3+6n^*f^2)+(4f+n^*)n^*f^4-(4f+n^*)^2(f^4+4n^*f^3) -(4f^3+6n^*f^2)^2} > 0 \tag{50}$$

and

$$-4n^{*3}f^{11}-f^{10}(n^{*4}+480n^{*2}) + f^9(32n^{*2}+ 576\alpha n^*-824n^{*3})$$
$$+f^8(16n^{*3}-528n^{*4}+704n^{*2}\alpha-256\alpha^2-1280\alpha+320n^*)$$
$$+f^7(816n^{*2}-152n^{*5}+128n^{*3}-64n^*-5184\alpha n^*+372\alpha n^{*3}$$
$$+256\alpha+2n^{*4}-256n^*\alpha^2)+f^6(65n^{*4}+632n^{*3}$$
$$-7424\alpha n^{*2}+1232n^{*2}+576\alpha n^*+90\alpha n^{*4}-16n^{*6}-96n^{*2}\alpha^2))$$
$$+f^5(208n^{*4}+2156n^{*3}+8n^{*5}-236\alpha n^{*2}+1024\alpha n^*$$
$$-2752\alpha n^{*3}+8n^{*5}\alpha-16n^{*3}\alpha^2)+f^4(24n^{*5}+2527n^{*4}$$
$$-384n^{*3}+2304\alpha n^{*2}-1344\alpha n^{*4}-n^{*4}\alpha^2+76\alpha n^{*3})$$
$$+f^3(832n^{*5}-96n^{*4}-1024n^{*3}-144\alpha n^{*5}+1344\alpha n^{*3}+6\alpha n^{*4})$$
$$+f^2(96n^{*6}-768n^{*4}+ 304\alpha n^{*4} -8n^{*5}) + f\,(24\alpha n^{*5}-192n^{*5})$$
$$- 16n^{*6} = 0. \tag{51}$$

Equation (51) will have no real positive root or it will have even number of real positive roots. If these satisfy equation (50), an even number of a points of bifurcation will exist.

5.5 BIFURCATION THEORY FOR THE GROWTH OF POPULATION IN THE PRESENCE OF POLLUTION

Following May (1973), we take

$$\frac{dN}{dt} = KN - bN^2 - CN \int_{-\infty}^{t} N(t')G(t-t')dt' \qquad (52)$$

the kernal function $G(t-t')$ gives the influence of the population at time t' on the population at time t.

Let $$G(t-t') = \frac{e^{-a(t-t')}(t-t')^{p-1}a^p}{\Gamma(p)}$$

and

$$Q_p(t) = \int_{-\infty}^{t} N(t') \frac{e^{-a(t-t')}(t-t')^{p-1}a^p}{\Gamma(p)} dt'$$

then we have

$$\frac{dN}{dt} = KN(t) - bN^2(t) - CN(t)\,Q_p(t)$$

$$\frac{dQ_p}{dt} = a(Q_{p-1}(t) - Q_p(t))$$

$$\frac{dQ_{p-1}}{dt} = a(Q_{p-2}(t) - Q_{p-1}(t))$$

. . . .

. . . .

$$\frac{dQ_2}{dt} = a(Q_1(t) - Q_2(t))$$

$$\frac{dQ_1}{dt} = a(N(t) - Q_1(t)) \qquad (53)$$

For equilibrium

$$\hat{N} = \frac{K}{b+C} = \hat{Q}_1 = \hat{Q}_2 \;\cdots\; \hat{Q}_p \tag{54}$$

The matrix A for the system is given by

$$\begin{bmatrix} -b\hat{N} & -C\hat{N} & 0 & 0 & 0 \;\cdots\; 0 & 0 \\ 0 & -a & a & 0 & 0 \;\cdots\; 0 & 0 \\ 0 & 0 & -a & a & 0 \;\cdots\; 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots \;\cdots\; \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 \quad -a & a \\ a & 0 & 0 & 0 & 0 \quad\;\; 0 & -a \end{bmatrix}$$

The equation for eigenvalues, on simplification, gives

$$\lambda^{p+1} + \lambda^{p}({}^{p}C_1 a + b\hat{N}) + \lambda^{p-1}({}^{p}C_2 a^2 + {}^{p}C_1 ab\hat{N})$$
$$+ \lambda^{p-2}({}^{p}C_3 a^3 + {}^{p}C_2 a^2 b\hat{N}) + \cdots$$
$$+ \; b\hat{N}a^p + a^p C\hat{N} = 0 \tag{55}$$

5.6 SPECIAL CASES

(i) $p = 1$

$$\lambda^2 + \lambda(a+b\hat{N}) + a\hat{N}(b+C) = 0 \tag{56}$$

(ii) $p = 2$

$$\lambda^3 + \lambda^2(2a+b\hat{N}) + \lambda(a^2+2ab\hat{N}) + a^2(b\hat{N}+C\hat{N}) = 0 \tag{57}$$

(iii) $p = 3$

$$\lambda^4 + \lambda^3(3a+b\hat{M}) + \lambda^2(3a^2+3ab\hat{N}) + \lambda(a^3+3a^2b\hat{N})$$
$$+ a^3(b\hat{N} + C\hat{N}) = 0 \tag{58}$$

(iv) p = 4

$$\lambda^5+\lambda^4(4a+b\hat{N})+\lambda^3(6a^2+4ab\hat{N}) + \lambda^2(4a^3+6a^2b\hat{N})$$
$$+\lambda(a^4+4b\hat{N}a^3) + a^4\hat{N}(b+C) = 0 \qquad (59)$$

For discussing the points of bifurcation, we apply conditions (13), (15), (17) and (19)

For $p = 1$

$$a+b\hat{N} = 0, \quad a\hat{N}(b+c) > 0 \qquad (60)$$

there is no real positive value of a so there will be no point of bifurcation.

For $p = 2$

$$2a^2+a(4b\hat{N}-C\hat{N}) + 2b^2\hat{N}^2 = 0 \qquad (61)$$

This equation either has no positive real root or gives even number of real positive roots. If it gives even number of positive real roots, there exist two points of bifurcation.

For $p = 3$

$$\frac{a^3+3a^2b\hat{N}}{3a+b\hat{N}} > 0 \qquad (62)$$

and

$$(a^3+3a^2b\hat{N})^2-(3a+b\hat{N})(3a^2+3ab\hat{N})(a^3+3a^2b\hat{N})$$
$$+a^3(b\hat{N}+C\hat{N})(3a+b\hat{N})^2 = 0 \qquad (63)$$

$$-8a^3+a^2\hat{N}(9C-24b)+a\hat{N}^2(6bC-24b^2) + \hat{N}^3(b^2C-8b^3) = 0$$
$$(64)$$

If $C/b > 8$, point of bifurcation exists if that value of a also satisfies eqn. (62).

If $C/b < 8$, then either there will exist no positive real root or there exist even number of positive real roots. If roots exist and satisfy eqn. (62) there will exist a point of bifurcation.

For $p = 4$ the required conditions are

$$\frac{(a^4+4b\hat{N}a^3)(4a+b\hat{N}) - a^4\hat{N}(b+C)}{(4a+b\hat{N})(6a^2+4ab\hat{N})-(4a^3+6a^2b\hat{N})} > 0 \qquad (65)$$

and

$$64a^4+\hat{N}a^3(256b-112C)+a^2\hat{N}^2(384b^2+144bC-C^2)$$
$$+a\hat{N}^3(256b^3-86b^2C)+\hat{N}^4(64b^4-16b^3C) = 0 \qquad (66)$$

If $4 < C/b$ there exists a real positive root. If this satisfies eqn. (65) there exist a point of bifurcation. If $4 > C/b$ then either there will exist no positive real root or there exist even number of positive real roots. If roots exist and satisfy eqn. (65) there will exist a point of bifurcation.

CHAPTER 6

TRANSITION FROM DETERMINISTIC TO STOCHASTIC MODELS

6.1 DETERMINISTIC AND STOCHASTIC MODELS

All the models considered so far in the thesis, whether in terms of differential equations or difference equations or integro-differential equations or delay-differential equations, have been deterministic i.e. our object has been to determine the population sizes of the various species as definite and uniquely defined functions of time. In these deterministic models for population growth, we seek to determine the population size $N(t)$ as a function of time. If the model is assumed correct, there is no uncertainity about $N(t)$.

In practice however chance plays an important role and very often we prefer to seek to determine $p(n,t)$ which is the probability of the population size being n at a given time t. Thus at a given time t, the population size does not have a fixed value but may take values $0,1,2,3,\ldots,n\ldots$ with probabilities $p(0,t)$, $p(1,t)$, $p(2,t)$, $p(3,t),\ldots,p(n,t)$ ... so that at any given time we seek to determine the probability distribution of the population size. We, of course get a family of probability distributions one probability distribution for each t. Such models for determining probability distributions are called stochastic models.

In the present chapter, we develop a general method of formulating the stochastic models, corresponding to a deterministic model given in terms of a system of differential equations. This method was first initiated by Kapur [1971].

The basic idea is to regard the positive terms in the expressions for the derivatives of population size as due to 'births' and the negative terms there as due to 'deaths', so that every system corresponds to a non-linear birth and death process. This approach gives in general an infinite system of differential-difference equations for determining the infinite set of probabilities $p(n,t)$. In general the differential equation determining $p(n,t)$ involves $p(n+1,t)$ and so if take a finite subset of equations, it cannot determine all the probabilities. As such we have to consider the infinite system of differential difference equation as a whole.

To solve the system we therefore take recourse to the use of probability generating function defined by

$$\phi(s,t) = \sum_{n=0}^{\infty} p(n,t)\, s^n$$

We determine a partial differential equation for solving for $\phi(s,t)$. If we can solve this equation, we can find $\phi(s,t)$ and then by expanding it in power of s, we can find $p(n,t)$. This method has been successfully applied to linear birth-death-immigration processes. However when the processes is non-linear or when emigration is involved, some difficulties arise in solving the resulting partial differential equation.

For linear birth-death-immigration, emigration process, a solution was given by Getz [1975]. However he omitted a term containing the probability of extinction and thus all his calculations were wrong. Later Kapur pointed out this mistake which was accepted by Getz [1978]. The following cases were discussed by Kapur.

(i) Birth-Death-emigration process : The complete solution was obtained in terms of incomplete beta function Kapur [1979a], [1979b].

(ii) Birth-Death-emigration process with birth rate less than death rate. The solution was obtain by solving an Abel's integral equation (Kapur and Saleem [1979]).

(iii) Birth-Death-immigration-emigration process : The complete solution for the steady case was obtain by Kapur [1978a, 1978b, 1979c, 1979d] and (Kapur and Kapur [1978]).

The processes which arise in general are non-linear and it is not possible to solve the partial differential equation for the probability generating function for the following reasons.

(a) The partial differential equation contains in addition to the unknown function $\phi(s,t)$ some terms involving unknown probabilities.

(b) The partial differential equations are highly non-linear.

(c) We have the initial constrains in the form

$$\phi(s,0) = S^{n_0}$$

where n_0 is the initial number of person in the system, but no boundary conditions are given so that for the steady case we have to solve partial differential equation without any initial and boundary conditions.

We have investigated the partial differential equations which arise in a number of problems. We have not attempted to solve these. However we have obtained with their help differential equations for moments for the probability distributions. Unfortunately again here the system becomes indeterminate in the sense that the number of unknown moments to be found out are always more than the number of equations. We can however integrate these in some cases to obtain some interesting relations between the moments.

6.2 FORMATION OF THE STOCHASTIC MODEL CORRESPONDING TO A GIVEN DETERMINISTIC MODEL

Consider a general deterministic model

$$\dot{X}_i = \sum_{j=1}^{n} a_{ij} X_j - X_i \sum_{j=1}^{n} b_{ij} X_j + c_i \quad (i = 1,2,\ldots,n) \tag{1}$$

Here all the coefficients are positive. Let $p(X_1,X_2,\ldots,X_n,t)$ be the probability that at time t, there are X_1 individuals of the first kind, X_2 individuals of the second kind and so on. Also we assume

$$P(\text{birth of an individual of the ith species in time } \Delta t)$$

$$= \left(\sum_{j=1}^{n} a_{ij} X_j + c_i\right) \Delta t + O[(\Delta t)^2].$$

P (death of an individual of the ith species in time Δt)

$$= \left(\sum_{j=1}^{n} b_{ij} X_i X_j\right) \Delta t + 0[(\Delta t)]^2.$$

P (more than one change in time $\Delta t = 0(\Delta t)$)

so that probability of no change in time Δt

$$= 1 - \left(\sum_{i=1}^{n}\sum_{j=1}^{n} a_{ij}X_j + \sum_{i=1}^{n} c_i\right)\Delta t - \left(\sum_{i=1}^{n}\sum_{j=1}^{n} b_{ij}X_iX_j\right)\Delta t + 0[(\Delta t)]^2 \qquad (2)$$

We then get,

$$p(X_1,X_2,\ldots,X_n,t+\Delta t) = p(X_1,X_2,\ldots,X_n,t)\Big[1-\Big(\sum_{i=1}^{n}\sum_{j=1}^{n} a_{ij}X_j + \sum_{i=1}^{n} c_i\Big)\Delta t - \Big(\sum_{i=1}^{n}\sum_{j=1}^{n} b_{ij}X_iX_j\Big)\Delta t\Big]$$

$$+ \sum_{i=1}^{n} p(X_1,X_2,\ldots,X_i-1,X_{i+1}\ldots X_n,t)\Big[\sum_{\substack{j=1\\ j\neq i}}^{n} a_{ij}X_j + a_{ii}(X_i-1) + c_i\Big]\Delta t$$

$$+ \sum_{j=1}^{n} p(X_1,X_2,\ldots,X_i+1, X_{i+1}\ldots X_n,t)\Big[\sum_{j=1}^{n} b_{ij}X_j(X_i+1)\Big]\Delta t + 0[\Delta t]^2 \qquad (3)$$

Proceeding to the limit as $\Delta t \to 0$, we get

$$\frac{d}{dt} p(X_1,X_2,\ldots,X_n,t) = -p(X_1,X_2,\ldots,X_n,t) \left[\sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} X_j + \sum_{i=1}^{n} c_i \right]$$

$$- p(X_1,X_2,\ldots,X_n,t) \sum_{i=1}^{n} \sum_{j=1}^{n} b_{ij} X_i X_j$$

$$+ \sum_{i=1}^{n} p(X_1,X_2,\ldots,X_i-1,X_{i+1},\ldots,X_n,t)$$

$$\left[\sum_{\substack{j=1\\ j\neq i}}^{n} a_{ij} X_j + c_i + a_{ii} (X_i-1) \right]$$

$$+ \sum_{i=1}^{n} p(X_1,X_2,\ldots,X_i+1,X_{i+1},\ldots,X_n,t)$$

$$\left[\sum_{\substack{j=1\\ j\neq i}}^{n} b_{ij}(X_i+1)X_j + b_{ii}(X_i+1)^2 \right]$$

$$= -p(X_1,X_2,\ldots,X_n,t) \left[\sum_{i=1}^{n} \sum_{j=1}^{n} a_{ij} X_j + \sum_{i=1}^{n} c_i \right]$$

$$- p(X_1,X_2,\ldots,X_n,t) \sum_{i=1}^{n} \sum_{j=1}^{n} b_{ij} X_i X_j$$

$$+ \sum_{i=1}^{n} p(X_1,X_2,\ldots,X_i-1,X_{i+1},\ldots,X_n,t)$$

$$\left[\sum_{j=1}^{n} a_{ij} X_j - a_{ii} + c_i \right]$$

$$+ \sum_{i=1}^{n} p(X_1, X_2, \ldots, X_{i}+1, X_{i+1}, \ldots, X_n, t) \left[\sum_{j=1}^{n} b_{ij}(X_i+1)\, X_j + b_{ii}\,(X_i+1)^2 \right] \qquad (4)$$

These equations will hold for values of $X_1, X_2, \ldots, X_n$ from 1 to ∞ with slight modifications, these will also hold for the cases when some X's are zero.

Now we define the generating function

$$\phi(s_1, s_2, \ldots, s_n, t) = \sum_{X_n=0}^{\infty} \cdots \sum_{X_2=0}^{\infty} \sum_{X_1=0}^{\infty} p(X_1, X_2, \ldots, X_n, t) \,.\, s_1^{X_1} \,.\, s_2^{X_2} \ldots s_n^{X_n} \qquad (5)$$

Multiplying (4) by $s_1^{X_1} \,.\, s_2^{X_2} \ldots s_n^{X_n}$ and summing up for all X's, we get

$$\frac{\partial\phi}{\partial t} = -\sum_{j=1}^{n} \sum_{i=1}^{n} a_{ij}\, s_j (1-s_i) \frac{\partial\phi}{\partial s_j} + \sum_{j=1}^{n} \sum_{i=1}^{n} b_{ij}\, s_j (1-s_i) \frac{\partial^2\phi}{\partial s_i \partial s_j}$$

$$+ \sum_{i=1}^{n} b_{ii}\,(1-s_i) \frac{\partial\phi}{\partial s_i} - \phi \sum_{i=1}^{n} c_i\,(1-s_i) \qquad (6)$$

+ some terms independent of ϕ .

If there are $X_1^0, X_2^0, \ldots, X_n^0$ individuals at time $t = 0$, we get the initial condition

$$\phi(s_1, s_2, \ldots, s_n, 0) = s_1^{X_1^0}\, s_2^{X_2^0}, \ldots, s_n^{X_n^0} \,. \qquad (7)$$

6.3 COMPETITION FOR FOOD BETWEEN TWO SPECIES

$$\frac{dX}{dt} = aX - bXY$$

$$\frac{dY}{dt} = PY - cXY \qquad (8)$$

In the absence of other species, each species grows exponentially and both species complete for the same food. Hence all the coefficients are positive.

Let $p(X,Y,t)$ be the probability that at time t, there are X individuals for the first kind and Y individuals for the second kind. Also we assume

Birth of the first species at time t = aX

Death of the first species at time t = bXY

Birth of the second species at time t = PY

Death of the second species at time t = cXY

Probability of more than one change in time $\Delta t = O(\Delta t)$ we then get,

$$\begin{aligned} p(X,Y,t+\Delta t) &= p(X-1,Y,t)\left[a(X-1)\,\Delta t + O\{(\Delta t)^2\}\right] \\ &+ p(X+1,Y,t)\left[b(X+1)Y\,\Delta t + O(\Delta t)\right] \\ &+ p(X,Y-1,t)\left[p(Y-1)\,\Delta t + O\{(\Delta t)^2\}\right] + p(X,Y+1,t) \\ &\left[cX(Y+1)\,\Delta t + O\{(\Delta t)^2\}\right] + p(X,Y,t)\left[1-(aX+bXY\right. \\ &\left.+ PY + cXY)\right]\Delta t + O\{(\Delta t)^2\} \end{aligned} \qquad (9)$$

Proceeding to the limit $\Delta t \to 0$, we get

$$\frac{d}{dt} p(X,Y,t) = p(X-1,Y,t)(X-1)a + p(X+1,Y,t)(X+1)Yb$$
$$+ p(X,Y-1,t)(Y-1)P + p(X,Y+1,t)X(Y+1)c$$
$$- p(X,Y,t)\left[aX + bXY + PY + cXY\right] \qquad (10)$$

$X = 1,2,3 \ldots$
$Y = 1,2,3 \ldots$

Similarly when the population of first species is zero, we get

$$\frac{d}{dt} p(0,Y,t) = p(1,Y,t)Yb + p(0,Y-1,t)(Y-1)P - P(0,Y,t)YP$$
$$Y = 1,2,3 \ldots \qquad (11)$$

When the population of the second species is zero

$$\frac{d}{dt} p(X,0,t) = p(X-1,0,t)(X-1)a + p(X,1,t)Xc - p(X,0,t)Xa$$
$$X = 1,2,3 \ldots \qquad (12)$$

and when populations of both species are zero at time t we get

$$\frac{d}{dt} p(0,0,t) = 0 \qquad (13)$$

Summing (10), (11), (12) and (13), we get

$$\frac{d}{dt} p(X,Y,t) = \sum_{X=1}^{\infty}\sum_{Y=1}^{\infty} p(X-1,Y,t)\,a(X-1) + \sum_{X=1}^{\infty}\sum_{Y=1}^{\infty} p(X+1,Y,t)(X+1)Yb$$
$$+ \sum_{X=1}^{\infty}\sum_{Y=1}^{\infty} p(X,Y-1,t)(Y-1)P + \sum_{X=1}^{\infty}\sum_{Y=1}^{\infty} p(X,Y+1,t)X(Y+1)c$$
$$- \sum_{X=1}^{\infty}\sum_{Y=1}^{\infty} p(X,Y,t)\,(aX+PY+bXY + cXY)$$
$$+ \sum_{Y=1}^{\infty} p(1,Y,t)\,bY + \sum_{Y=1}^{\infty} p(0,Y-1,t)(Y-1)P$$

$$- \sum_{Y=1}^{\infty} p(0,Y,t)\, Yp + \sum_{X=1}^{\infty} p(X-1,0,t)\,(X-1)a$$

$$+ \sum_{X=1}^{\infty} p(X,1,t)\, Xc - \sum_{X=1}^{\infty} p(X,0,t)\, Xa \qquad (14)$$

Now we define the generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty} \sum_{Y=0}^{\infty} p(X,Y,t)\, z^X s^Y \qquad (15)$$

equation (11) by s^Y, equation

Multiplying equation (10) throughout by $z^X s^Y$ and summing for all X and Y, we get with the help of (15)

$$\frac{\partial \phi}{\partial t} = P(s-1)s \frac{\partial \phi}{\partial s} + cz\,(1-s) \frac{\partial^2 \phi}{\partial z \partial s} +$$

$$bs(1-z) \frac{\partial^2 \phi}{\partial s \partial z} + az\,(z-1) \frac{\partial \phi}{\partial z} \qquad (16)$$

6.4 LAUNCHESTER MODEL FOR A BATTLE

$$\frac{dX}{dt} = P - aY$$

$$\frac{dY}{dt} = q - bX \qquad (17)$$

where X and Y are the numbers of effective attacker and defender troop, P and q are the rates at which they are being reinforced and a and b are attacker and defender casualities per opposing combatant.

Resulting partial differential equation by taking generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty} \sum_{Y=0}^{\infty} p(X,Y,t)\, z^X s^Y \qquad (18)$$

is given by

$$\frac{\partial \phi}{\partial t} = \frac{\partial \phi}{\partial s}\left[\frac{as}{z} - as\right] + \frac{\partial \phi}{\partial z}\left[\frac{bz}{s} - bz\right]$$

$$a\left[\sum_{Y=1}^{\infty} Y\, p(0,Y,t)\, s^{Y}\left(1 - \frac{1}{z}\right)\right]$$

$$+ b\left[\sum_{X=1}^{\infty} X\, p(X,0,t)\, z^{X}\left(1 - \frac{1}{s}\right)\right]$$

$$+ q\phi\,(s-1) + p\phi\,(z-1) \tag{19}$$

6.5 MODEL FOR INTERNATIONAL TRADE *

$$\frac{dX}{dt} = -aX + bXY$$

$$\frac{dY}{dt} = -PY + cXY \tag{20}$$

Here trade is beneficial to both nations and isolation is harmful.

Resulting partial differential equation by taking generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty}\sum_{Y=0}^{\infty} p(X,Y,t)\, z^{X} s^{Y} \tag{21}$$

is given by

$$\frac{\partial \phi}{\partial t} = \frac{\partial \phi}{\partial s}\left[P(1-s)\right] + \frac{\partial \phi}{\partial z}\left[a(1-z)\right]$$

$$+ \frac{\partial^{2} \phi}{\partial z \partial s}\left[bz(z-1)s + cz\, s(s-1)\right] \tag{22}$$

6.6 PREDATOR-PREY MODEL

$$\frac{dX}{dt} = aX - bXY$$
$$\frac{dY}{dt} = cXY - PY \tag{23}$$

Here X, Y are the two populations at time t. In the absence of Y species the species X grows exponentially while in the absence of X species, the species Y decreases exponentially. The mutual contacts are useful for Y and harmful for X species.

By taking generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty} \sum_{Y=0}^{\infty} p(X,Y,t)\, z^X s^Y \tag{24}$$

the resulting partial differential equation is

$$\frac{\partial \phi}{\partial t} = \frac{\partial \phi}{\partial s}\left[P(1-s)\right] + \frac{\partial \phi}{\partial z}\left[az\,(z-1)\right] + \frac{\partial^2 \phi}{\partial z \partial s}\left[cz\, s(s-1) + bs\,(1-z)\right] \tag{25}$$

6.7 MEMBERSHIP OF POLITICAL PARTIES

$$\frac{dX}{dt} = aX - bY + c$$
$$\frac{dY}{dt} = -PX + qY + r \tag{26}$$

Here the membership of a political party has an encouraging effect on its own strength and the membership of the opposite political party has an inhibiting effect.

Resulting partial differential equation by taking generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty} \sum_{Y=0}^{\infty} p(X,Y,t)\ z^X s^Y \tag{27}$$

is given by

$$\frac{\partial\phi}{\partial t} = \frac{\partial\phi}{\partial s}\left[qs(s-1) + bs(\tfrac{1}{z} - 1)\right] + \frac{\partial\phi}{\partial z}\left[az\ (z-1) + \frac{Pz}{s} - Pz\right]$$
$$+ \phi\left[r(s-1) + c(z-1)\right] + b \sum_{Y=1}^{\infty} Y\ p(0,Y,t)\ s^Y\ (1 - \tfrac{1}{z})$$
$$+ P \sum_{X=1}^{\infty} X\ p(X,0,t)\ z^X\ (1 - \tfrac{1}{s}) \tag{28}$$

6.8 ARMS RACE BETWEEN TWO NATIONS

$$\begin{aligned} \frac{dX}{dt} &= -\ aX + bY + c \\ \frac{dY}{dt} &= PX - qY + r \end{aligned} \tag{29}$$

The rate at which a nation build up its armed-strength is proportional to the armed strength of the enemy and also to its own, the rate is positively correlated with enemy strength and negatively correlated with its own.

The resulting partial differential equation by taking generating function

$$\phi(z,s,t) = \sum_{X=0}^{\infty} \sum_{Y=0}^{\infty} p(X,Y,t)\ z^X s^Y \tag{30}$$

is given by

$$\frac{\partial\phi}{\partial t} = \frac{\partial\phi}{\partial s}\left[q(1-s) + bs(z-1)\right] + \frac{\partial\phi}{\partial z}\left[Pz\,(s-1) + a(1-z)\right]$$

$$+ \quad \phi\left[c(z-1) + r(s-1)\right] \qquad (31)$$

6.9 MOMENTS OF PROBABILITY DISTRIBUTION

To deduce the moments, we use the relations

$$E(Y) = \frac{\partial\phi}{\partial s} \qquad E(X) = \frac{\partial\phi}{\partial z} \qquad E(XY) = \frac{\partial^2\phi}{\partial z\,\partial s} \qquad (32)$$

$$E(Y^2) = \frac{\partial^2\phi}{\partial s^2} + \frac{\partial\phi}{\partial s}, \quad E(X^2) = \frac{\partial^2\phi}{\partial z^2} + \frac{\partial\phi}{\partial z}$$

$$Var(Y) = \frac{\partial^2\phi}{\partial s^2} + \frac{\partial\phi}{\partial s} - \left(\frac{\partial\phi}{\partial s}\right)^2, \quad Var(X) = \frac{\partial^2\phi}{\partial z^2} + \frac{\partial\phi}{\partial z} - \left(\frac{\partial\phi}{\partial z}\right)^2 \qquad (33)$$

where all the partial derivatives are evaluated at $s = 1$, $z = 1$. For any model, to obtain the moments we differentiate the partial differential equation of the probability generating function for the model.

(i) Once with respect to s, once with respect to z and then put $s = 1$, $z = 1$.

(ii) Twice with respect to s, twice with respect to z, once with respect to s and then with respect to z and then put $s = z = 1$ and so on.

Using this method we get the following relations

(a) ARMS RACE BETWEEN TWO NATIONS

$$\frac{d}{dt}\,E(X) = b\,E(Y) - a\,E(X) + c \qquad (34)$$

$$\frac{d}{dt} E(Y) = -q\,E(Y) + PE(X) + r \tag{35}$$

$$\frac{d}{dt} E(X^2) = aE(X) + bE(Y) + 2c\,E(X) + 2b\,E(XY) - 2a\,E(X^2) + c \tag{36}$$

$$\frac{d}{dt} E(Y^2) = qE(Y) + 2rE(Y) + PE(X) + 2PE(XY) - 2q\,E(Y^2) + r \tag{37}$$

$$\frac{d}{dt} E(XY) = bE(Y^2) + PE(X^2) - (a+q)\,E(XY) + cE(Y) + rE(X) \tag{38}$$

(b) INTERNATIONAL TRADE

$$\frac{d}{dt} E(X) = -a\,E(X) + b\,E(XY) \tag{39}$$

$$\frac{d}{dt} E(Y) = -P\,E(Y) + c\,E(XY) \tag{40}$$

$$\frac{d}{dt} E(X^2) = a\,E(X) + \cancel{2}b\,E(XY) - 2a\,E(X^2) + 2bE(X^2Y) \tag{41}$$

$$\frac{d}{dt} E(Y^2) = PE(Y) + \cancel{2}c\,E(XY) - 2P\,E(Y^2) + 2c\,E(XY^2) \tag{42}$$

$$\frac{d}{dt} E(XY) = -(P+a)\,E(XY) + c\,E(X^2Y) + bE(XY^2) \tag{43}$$

(c) PREDATOR - PREY MODEL

$$\frac{d}{dt} E(X) = aE(X) - bE(XY) \tag{44}$$

$$\frac{d}{dt} E(Y) = -PE(Y) + cE(XY) \tag{45}$$

$$\frac{d}{dt} E(X^2) = aE(X) + bE(XY) + 2aE(X^2) - 2bE(X^2Y) \tag{46}$$

$$\frac{d}{dt} E(Y^2) = PE(Y) + cE(XY) - 2PE(Y^2) + 2cE(Y^2X) \tag{47}$$

$$\frac{d}{dt} E(XY) = (a-P)\ E(XY) + cE(X^2Y) - bE(XY^2) \tag{48}$$

(d) COMPETITION MODEL

$$\frac{d}{dt} E(X) = aE(X) - bE(XY) \tag{49}$$

$$\frac{d}{dt} E(Y) = PE(Y) - cE(XY) \tag{50}$$

$$\frac{d}{dt} E(X^2) = aE(X) + 2aE(X^2) + bE(XY) - 2bE(X^2Y) \tag{51}$$

$$\frac{d}{dt} E(Y^2) = PE(Y) + 2PE(Y^2) + cE(XY) - 2cE(XY^2) \tag{52}$$

$$\frac{d}{dt} E(XY) = (P+a)\ E(XY) - bE(XY^2) - cE(X^2Y) \tag{53}$$

(e) LAUNCHESTER MODEL

$$\frac{d}{dt} E(X) = -aE(Y) + a \sum_{Y=1}^{\infty} Y\, p(0,Y,t) + P \tag{54}$$

$$\frac{d}{dt} E(Y) = -bE(X) + b \sum_{X=1}^{\infty} X\, p(X,0,t) + q \tag{55}$$

$$\frac{d}{dt} E(X^2) = aE(Y) - a \sum_{Y=1}^{\infty} Y\, p(0,Y,t) + 2PE(X) - 2aE(XY) + P \tag{56}$$

$$\frac{d}{dt} E(Y^2) = bE(X) - b \sum_{X=1}^{\infty} X\, p(X,0,t) + 2q\ E(Y) - 2bE(XY) + q \tag{57}$$

$$\frac{d}{dt} E(XY) = -aE(Y^2) - bE(X^2) + qE(X)$$

$$+ PE(Y) + a \sum_{Y=1}^{\infty} Y^2 \, p(0,Y,t) + b \sum_{X=1}^{\infty} X^2 \, p(X,0,t) \qquad (58)$$

(f) MEMBERS OF POLITICAL PARTIES

$$\frac{d}{dt} E(X) = aE(X) - bE(Y) + b \sum_{Y=1}^{\infty} Y \, p(0,Y,t) + c \qquad (59)$$

$$\frac{d}{dt} E(Y) = qE(Y) - PE(X) + P \sum_{X=1}^{\infty} X \, p(X,0,t) + r \qquad (60)$$

$$\frac{d}{dt} E(X^2) = (2c+a)\, E(X) + bE(Y) - 2bE(XY)$$

$$+ 2aE(X^2) - b \sum_{Y=1}^{\infty} Y \, p(0,Y,t) + c \qquad (61)$$

$$\frac{d}{dt} E(Y^2) = (q + 2r)\, E(Y) + PE(X) + 2qE(Y^2)$$

$$- 2PE(XY) - P \sum_{X=1}^{\infty} X \, p(X,0,t) + r \qquad (62)$$

$$\frac{d}{dt} E(XY) = (q+a)\, E(XY) - PE(X^2) - bE(Y^2)$$

$$+ \cancel{PE(X^2 Y)} + rE(X) + cE(Y) + b \sum_{Y=1}^{\infty} Y^2 \, p(0,Y,t)$$

$$+ P \sum_{X=1}^{\infty} X^2 \, p(X,0,t) \qquad (63)$$

6.10 RELATION BETWEEN MOMENTS

(i) ARMS RACE BETWEEN TWO NATIONS

We choose ℓ and m positive constants to satisfy relation (64)

$$\frac{mp - a\ell}{\ell} = \frac{\ell b - mq}{m} \tag{64}$$

then we get from equation (29)

$$\frac{d}{dt}\left[\ell E(X) + mE(Y)\right] = k\left[\ell E(X) + mE(Y)\right] + \ell c + mr \tag{65}$$

where

$$\ell = (q-a) + \sqrt{(q-a)^2 + 4bP}, \quad m = 2b \tag{66}$$

$$k = \frac{\sqrt{(q-a)^2 + 4bP} - (q+a)}{2} \tag{67}$$

On integrating equation (65), we get

$$\ell E(X) + mE(Y) = \left[\ell X_0 + mY_0\right] e^{kt} + \frac{\ell c + mr}{k}(e^{kt} - 1) \tag{68}$$

where X_0 and Y_0 are the initial values of X and Y.

Equation (68) shows that $\ell E(X) + mE(Y)$ will increase or decrease asemptotically with time according as

$$bP \gtrless aq \tag{69}$$

We may note that for the deterministic model

$$\ell X + mY = (\ell X_0 + mY_0)\, e^{kt} + \frac{\ell c + mr}{k}(e^{kt} - 1) \tag{70}$$

so that $\ell X + mY$ for the deterministic model and $\ell E(X) + mE(Y)$ for the stochastic model are identical function of time. This is obvious otherwise since X, Y and E(X), E(Y) satisfy the same differential equations. In this case from (34) and (35),

we can find $E(X)$ and $E(Y)$ as function of time and then can obtain $E(X^2)$, $E(Y^2)$, $E(XY)$ from (36), (37) and (38).

(ii) FOR INTERNATIONAL TRADE

From Equation ~~(20)~~, we get

$$\frac{d}{dt}\left[cE(X) - bE(Y)\right] = bPE(Y) - acE(X) \tag{71}$$

This corresponds to the equation

$$\frac{d}{dt}(cX - bY) = bPY - acX \tag{72}$$

for the deterministic model.

If however $a = P$, we get

$$\frac{d}{dt}\left[cE(X) - bE(Y)\right] = -a\left[cE(X) - bE(Y)\right] \tag{73}$$

so that

$$cE(X) - bE(Y) = (cX_o - bY_o)\, e^{-at} \tag{74}$$

and $cE(X) - bE(Y)$ decreases exponentially with time and

$$\underset{t \to \infty}{\mathrm{Lt}}\left[cE(X) - bE(Y)\right] = 0 \tag{75}$$

(iii) FOR PREDATOR-PREY MODEL

(44) and (45)

From equation ~~(23)~~, we get

$$\frac{d}{dt}\left[cE(X) + bE(Y)\right] = acE(X) - bPE(Y) \tag{76}$$

This corresponds to the equation

$$\frac{d}{dt}\left[cX + bY\right] = acX - bPY \tag{77}$$

for the deterministic model.

(iv) FOR THE COMPETITION MODEL

From equation (8), we get

$$\frac{d}{dt}\left[cE(X) - bE(Y)\right] = acE(X) - bPE(Y) \qquad (78)$$

This corresponds to

$$\frac{d}{dt}\left[cX - bY\right] = acX - bPY \qquad (79)$$

for the deterministic model.

If $a = P$, we get

$$\frac{d}{dt}\left[cE(X) - bE(Y)\right] = a\left[cE(X) - bE(Y)\right] \qquad (80)$$

so that

$$cE(X) - bE(Y) = (cX_0 - bY_0)\, e^{at} \qquad (81)$$

Thus $cE(X) - bE(Y)$ increases exponentially with time unless

$$cX_0 = bY_0$$

(a) If $cX_0 = bY_0$ then $cE(X) = bE(Y)$ for all t (82)

(b) If $cX_0 > bY_0$ then $cE(X) > bE(Y)$ for all t (83)

and

$$cE(X) - bE(Y) \to \infty \text{ and } t \to \infty \qquad (84)$$

In this case for the deterministic model $X \to \infty$, $Y \to 0$.

(c) If $cX_0 < bY_0$ then $cE(X) < bE(Y)$ for all t and

$$cE(X) - bE(Y) \to -\infty \text{ and } t \to \infty \qquad (85)$$

In this case for the deterministic model $X \to 0$, $Y \to \infty$.

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